THE UNIVERSITY OF ALBERTA

ODE MODELS OF A MUTUALIST INTERACTING IN ECOLOGICAL SYSTEMS

by

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To the loving memories of my parents Late Smt. Barmati Devi and Late Sri Permanand Rai and dearest *NANI* (Grandmother), Late Smt. Nagesara Kunwar.

ABSTRACT

The main purpose of this manuscript is to model and mathematically analyze the effect of a mutualist on a population by its interaction with a third population. Hence predator-prey-mutualist and a competitor-competitor-mutualist models are considered. In each case conditions for equilibria are given, and the stability of these equilibria analyzed. As well, conditions giving rise to periodic oscillations are determined. Results are interpreted biologically, and specific examples are given.

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CHAPTER I

INTRODUCTION

Mathematical models in theoretical ecology, like models in other branches of science, are useful, because they both answer and raise questions. Research in this area started with the celebrated works of Lotka (1925) and Volterra (1931), who mostly dealt with the models of predation and competition. This fact, together with the literature in the field such as Darwin (1902) and Gause (1934) were enough to dominate the way of thinking of the scientists working in these areas. The result was an emphasis on the struggle for existence. Another side of nature was ignored, where there existed a variety of fascinating co-operative associations, even between two entirely different types of organisms. This pattern continues today in that most books on ecology pay only token attention to symbiosis, whereas full chapters are devoted to predator-prey, food chains and models of competition (Risch and Boucher, 1970).

In its broadest sense, symbiosis is comprised of several types of close associations between organisms. One of the most common types of symbiosis, known as 'commensalism' is the relationship from which only one of the partners benefits, while the other is neither benefited nor harmed. As an example we can consider the association between sharks and the pilot fish (Simon, 1970). The association between them is commensal because the shark does not get anything from this association while the pilot fish are not only helped in getting food

from the scraps of the shark's meal but also they enjoy security against several predators which might otherwise prey upon them.

The symbiotic relation between two species, in which both the species benefit, has been termed as 'mutualism'. Sometimes the presence of a third species is required before the mutualism between two species can be apparent. For example, in the aphid-ant system, the association seems to be commensal, but considering that predators may prey on aphids in the absence of ants, the association is clearly mutualistic.

Mutualism is further subdivided into obligate and non-obligate mutualism. If the mutualistic interaction is crucial for the survival on one or both of the species then the mutualism is referred as obligate. As an example of non-obligate mutualism we can consider the association between the African crocodile and the Egyptian plover, commonly known as the crocodile-bird. The bird feeds on various parasites from the crocodile's skin and the scraps of meat sticking to the reptile's teeth. It thereby offers a cleaning service to the crocodile. An example of obligate-mutualism was demonstrated by Limbaugh (1964) and Eibl-Eibesfeldt (Simon, 1970). It was discovered that the association between certain species of large fishes and relatively smaller fishes, known as cleaner fishes, is essential for the good health of the former. To know how important is cleaning for the large fishes, Limbaugh removed all the cleaner fishes from a few small coral reefs in the Bahamas. After two weeks, all except those fish that habitually lived in the reefs were gone and those who stayed developed sores and swellings. He concluded that the cleaning is indeed vital to the health of fish. This phenomenon is known as 'cleaning-symbiosis'.

Recently mutualism has received more and more attention (e.g. Addicott 1979, 1981; Colwell and Fuentes 1975; Halam 1980; Huchinson 1978; May 1976; Risch and Boucher 1976; Roughgarden 1975; Vandermeer and Boucher 1978; Wilson 1980) as an important factor governing the populations of the interacting species. However, the mathematical theory needed to analyze such models is not yet developed.

Kolmogorov-type models of species interaction were used by Rescigno and Richardson (1967) for the study of two-dimensional mutualism. They established conditions under which the interior equilibrium is asymptotically stable. Later it was shown by Albrecht et al (1974) that the above mentioned equilibrium is globally asymptotically stable in the first quadrant. The study of two-dimensional Lotka-Volterra models of mutualism (Vandermeer and Boucher, 1978) has indicated that there are cases in which both populations survive, others where extinction is inevitable, and yet others in which the behaviour depends upon the initial populations. Computer simulation studies (Addicott, 1981) of models of two-dimensional mutualism has shown that these models are relatively more stable than models without mutualism. Basically, no general conclusions can be drawn for such models. Their stability behaviour depends upon the particular model studied. However, no model has been shown to exhibit periodic oscillation.

There are many cases in which mutualism enters a system due to the presence of a third species. A mutualist of a prey may decrease the predation of its predators, or compete with its predators. A mutualist of a predator may increase predation on the prey, or stimulate

the prey to more rapid growth. A mutualist of a species may help it to outcompete its competitors by aiding it directly, competing with the competitors, or predating on the competitors. It is for these reasons, three-species models are important.

This thesis is an analysis of the dynamics and stability of mutualism. The models treated here involve interactions among three species, depicting non-obligate mutualism between two of them. These are not just an extension of the two species mutualism to three species mutualism. In Chapter II, we mention some important theorems and the techniques which are used in the analysis of the models in the following two chapters. In Chapter III, we consider a model of predation in which there is also a mutualist to the prey. We assume here that the mutualist reduces the effect of predators on the prey. This could be accomplised in two ways: either by making prey more difficult to capture (e.g. Bequaert 1921; Culver and Beattie 1978; Janzen 1976) or by deterring the predator from feeding upon the prey (e.g. Bently 1976, 1977; Berger 1980; Bloom 1975; Glynn 1976; Ross 1971; Way 1963). The main result of this chapter is a Hopf-Bifurcation theorem, which predicts the appearance of small amplitude periodic solutions of the system under consideration, when one of the parameters passes through a certain critical value. We have also located the various equilibrium states and performed their local stability analysis. Then a special case of the general model has been considered in greater detail.

In Chapter IV, we consider another model incorporating two competing species and a mutualist to one of the competitors. Again there are several ways in which the mutualist can modify the competitive

interaction, but the one which has been depicted in the model is by decreasing the effect of the other competitor. For this model also we enunciate a Hopf-Bifurcation theorem, predicting the appearance of small amplitude periodic oscillations. Next, by taking a special case of the general model, we have been able to get several interesting results. Also, the various possible cases dealt with in Freedman (1980) for two-dimensional Lotka-Volterra competition models have been considered in the light of a third species (mutualist) and it has been shown that the mutualist plays a very important role, including the reversal of stability of the equilibrium states in some cases.

CHAPTER II

MATHEMATICAL PRELIMINARIES

In this chapter we shall mention various results from analysis and ordinary differential equations which we shall have occasion to use in the following chapters. The proofs of the theorems are not given, but references to where they may be found are mentioned. Few definitions are given, but the definitions of the undefined terms and other relevant details can be found in the cited references.

2.1. Characteristic equation, eigenvalues and eigenvectors of a matrix.

Let $A = (a_{ij})$ $i,j = 1,2,\ldots,n$ be a $n \times n$ real matrix. The equation

$$\det(A-\lambda I) = \begin{vmatrix} a_{11}-\lambda & a_{12} & \cdots & a_{1n} \\ a_{21} & a_{22}-\lambda & \cdots & a_{2n} \\ \vdots & & & \\ a_{n1} & a_{n2} & \cdots & a_{nn}-\lambda \end{vmatrix} = 0, \tag{2.1}$$

where $\lambda \in \mathcal{F}$ (field of complex numbers), is called the characteristic equation of the matrix A. When expanded the above equation becomes a polynomial equation of degree n in λ, say

$$\lambda^n + a_1\lambda^{n-1} + a_2\lambda^{n-2} + \ldots + a_{n-1}\lambda + a_n = 0 \tag{2.2}$$

where the a's are sums of products of the a_{ij}'s.

The roots of the characteristic equation (2.1) are called the characteristic values or eigen-values of the matrix A. By the

fundamental theorem of algebra and its corollaries, it is established that there are exactly n complex numbers λ, not necessarily distinct from one another, which satisfy the equation (2.2).

The column vector $X_i = (x_{i1}, x_{i2}, \ldots, x_{in})^T$ is said to be an eigenvector associated with the eigenvalue λ_i, if it satisfies the following matrix equation

$$(A-\lambda_i I)X_i = \phi \tag{2.3}$$

where ϕ is the null matrix.

2.2. Norms.

In analysing the stability of any solution of a given system of differential equations, we require a measure of the distance between solutions at particular times; that is, of the distance between the vectors of solution values. Suppose that the vector function $X(t)$ with projections $X_1(t), \ldots, X_n(t)$, represents a solution vector of some system of first-order equations of dimension n. Several measures of the 'size' of $X(t)$ (for fixed t), called norms of X, are used. It is denoted by $||X||$ and in the simplest case it can coincide with the Euclidian length of the vector i.e. it is defined by the formula

$$||X|| = \left(\sum_{i=1}^{n} X_i^2\right)^{\frac{1}{2}} \tag{2.4}$$

Two other frequently encountered norms are

$$||X|| = \max_i |X_i| \tag{2.5}$$

and $$||X|| = \sum_{i=1}^{n} |x_i| \tag{2.6}$$

The norm has the following properties (shared by all)

(i) $||X|| \geq 0$ for all X

(ii) $||X|| = 0$ iff $X = 0$

(iii) $||\alpha X|| = |\alpha|\ ||X||$, α real or complex

$||X+Y|| \leq ||X|| + ||Y||$ (triangle inequality)

We also require a measure of size for matrices. Let A be an $n \times n$ matrix (a_{ij}) with real or complex elements. Then we define

$$||A|| = \sum_{i=1}^{n} \sum_{j=1}^{n} |a_{ij}| \tag{2.7}$$

2.3. Exponential function of a matrix.

Let A be an $n \times n$ matrix. Then e^A is defined by

$$e^A = I + \sum_{m=1}^{\infty} \frac{A^m}{m!} \tag{2.8}$$

The series in the right hand side is convergent for all A. It can be deduced from (2.8) that

(i) $||e^A|| \leq e^{\|A\|}$

(ii) $e^{\phi} = I$ where ϕ is the null matrix

(iii) $e^{-A} = (e^A)^{-1}$

(iv) $\frac{d}{dt} e^{At} = Ae^{At} = e^{At}A$

(v) $(e^{At})^T = e^{A^T t}$

(vi) Let the eigenvalues of A be $\lambda_1, \lambda_2, \ldots, \lambda_n$. Then for any γ such that $\gamma > \max_{1 \le i \le n} \mathrm{Re}(\lambda_i)$ there exists a constant $c > 0$ such that

$$\|e^{At}\| < ce^{\gamma t}, \quad t \geq 0 \tag{2.9}$$

2.4. Stability of linear equations with contant coefficients.

Consider the general autonomous linear system

$$X' = AX \tag{2.10}$$

We mention the following theorem from Coppel (1965), which has been used many times.

Theorem. The equation (2.10) is stable if and only if every characteristic root of the constant matrix A has real part not greater than zero, and those with zero real parts are of simple type. It is strongly stable if and only if every characteristic root of A is pure imaginary and of simple type. It is asymptotically stable if and only if every characteristic root of A has negative real part.

2.5. Liapunov function and stability theorem according to the first approximation.

Consider the function $V(x_1, \ldots, x_n)$, defined in the phase space of the variables $x_1, x_2, \ldots, x_n$. Let $X = (x_1, \ldots, x_n)$, then $V(X)$ is positive definite in a neighbourhood U of the origin if

$$V(X) > 0 \text{ for all } X \neq 0 \text{ in } U \text{ and } V(0) = 0.$$

If $V(X)$ is positive definite and has continuous partial derivatives, then for all small enough positive c, the following property holds.

I. $V(X) < c$ defines an open, bounded, connected region ψ_c which contains the origin and has $V(X) = c$ as its boundary; the diameter of ψ_c tends to zero with c; and when $c_1 < c_2$ the boundary of ψ_{c_1} is contained in ψ_{c_2}.

(Jordan and Smith, 1977).

Strong Liapunov function.

A function $V(x)$ is said to be a strong Liapunov function for the system (2.10) if

(i) $V(X)$ and its partial derivatives are continuous;

(ii) $V(X)$ is positive definite in some neighbourhood U of $X = 0$;

(iii) $V'(X) < 0$ along the solutions of the system (2.10).

<u>Stability Theorem</u>. (Barbashin 1970). Let us consider the systems

$$X' = AX + F(X), \quad \text{where} \quad F = (F_1, \ldots, F_n)^T \tag{2.11}$$

and

$$X' = AX \tag{2.12}$$

Suppose that $\sum_{i=1}^{n} F_i^2(X) \leq K^2 \left(\sum_{i=1}^{n} x_i^2\right)^{1+\alpha}$, where $\alpha > 0$ and K is a positive constant. If the roots of the characteristic equation of (2.12) have negative real parts then the zero solution of the system (2.11) is asymptotically stable.

Domain of asymptotic stability.

The region $R \subseteq U$ will be defined to be the domain of asymptotic stability if the Liapunov function $V(X)$ and $(-V'(X))$, where $V'(X)$ is the derivative of $V(X)$ along the trajectories, have the same property I.

2.6. Hopf bifurcation.

A well utilized bifurcation is the Hopf bifurcation, in which a fixed equilibrium state bifurcates to periodic orbits, as one of the parameters of the system under consideration passes through a critical value, termed a bifurcation value. Hopf bifurcation has found its applications in almost all branches of science, sometimes providing a useful explanation for the appearance of certain observed natural phenomena.

We now state the Hopf bifurcation theorem, which is applicable to the types of models we are going to deal with in the following chapters.

<u>Theorem</u>. (Hopf bifurcation in $\mathbb{R}^n$), [Marsden and McCracken 1976]. Let $f_\mu(X)$ be a vector field on $\mathbb{R}^n$ for each μ, which is C^k in (X,μ) and C^{k+1} in X for each μ $(k \geq 4)$. Suppose that $f_\mu(0) = 0$ for all μ and let $A(\mu) = f'_\mu(0)$ have two distinct, complex conjugate eigenvalues $\lambda(\mu)$, $\overline{\lambda(\mu)}$ for μ near 0, such that

(i) $\operatorname{Re} \lambda(0) = 0$, $\frac{d}{d\mu} (\operatorname{Re} \lambda(\mu))\Big|_{\mu=0} \neq 0$;

(ii) remaining eigenvalues of $A(\mu)$ at $\mu = 0$ have all, negative real parts.

Then

(A) There is a C^{k-2} function $\mu: (-\varepsilon,\varepsilon) \to \mathbb{R}$ such that $(s,0,\mu(s))$ is on a closed orbit of period $\approx \frac{2\pi}{|\lambda(0)|}$ and radius growing like $\sqrt{\mu(s)}$ for $s \neq 0$ and such that $\mu(0) = 0$.

(B) There is a neighbourhood U of $(0,0,0)$ in $\mathbb{R}^3$ such that any closed orbit in U is one of those above.

(C) If 0 satisfies a "vague attractor" condition for the vector field $f_0(x)$ then $\mu(s) > 0$ for $s \neq 0$ and the periodic orbits are asymptotically stable.

2.7. Routh-Hurwitz Criterion.

This criterion will be used to obtain conditions for the asymptotic stability of the equilibrium states. Consider the n^{th} order polynomial equation given by (2.2). Then a formal general condition (the Routh-Hurwitz Criterion) can now be written, in terms of the coefficients $a_1, a_2, \ldots, a_n$, which are necessary and sufficient to ensure that all the roots of the equation (2.2) have negative real parts.

In our case $n \leq 3$, so that we mention the explicit Routh-Hurwitz Criterion for $n = 2$ and 3.

$n = 2$

$$\lambda^2 + a_1\lambda + a_2 = 0 \tag{2.8}$$

Conditions: $a_1 > 0$; $a_2 > 0$

$n = 3$

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0 \tag{2.9}$$

Conditions: $a_1 > 0$; $a_3 > 0$; $a_1a_2 - a_3 > 0$

Also it can be shown that when

$$a_1 > 0, \quad a_3 > 0, \quad a_1a_2 - a_3 = 0$$

the equation (2.9) has one real (negative) and a pair of pure imaginary roots.

(Robert M. May, 1973).

2.8. Dulac's Theorem.

The following theorem was proved by Dulac (see Andronov et al., p. 205).

Let $F(x,y)$, $G(x,y)$, $B(x,y)$ have continuous second partial derivatives, and let D be a simply connected domain. Then if $[\frac{\partial(BF)}{\partial x} + \frac{\partial(BG)}{\partial y}]$ does not change sign in D and is not identically zero in any open subdomain of D, then the system $x' = F(x,y)$, $y' = G(x,y)$, has no simple closed curves in D which are unions of solutions of this system.

CHAPTER III

PREDATOR-PREY-MUTUALIST MODEL

3.1. General Model.

We suppose that under the assumption of continuous birth and death rates the dynamics of population-growth of a predator-prey-mutualist system is governed by the following system of autonomous ordinary differential equations:

$$u' = uh(u,x) \tag{3.1a}$$

$$x' = \alpha x g(x,u) - yp(x,u) \tag{3.1b}$$

$$y' = y(-s+cp(x,u)) \quad \text{where } u,x \text{ form a mutualistic pair} \tag{3.1c}$$

$' = \frac{d}{dt}$ and t denotes time.

u = the number of mutualists at time t

x = the number of prey at time t

y = the number of predators at time t

$h(u,x)$ = specific growth rate of the mutualist in the presence of the prey

$\alpha g(x,u)$ = specific growth rate of the prey in the presence of the mutualist but in the absence of the predator

$p(x,u)$ = predator functional response

$s > 0$, $\alpha > 0$, $c > 0$ are parameters.

We shall assume that

$$u,x,y \in R_+$$

and

$$h,g,p: R_+ x R_+ \to R,$$

are continuous and sufficiently smooth functions to guarantee existence and uniqueness of initial value problems for (3.1) with the initial conditions $\in R_+^3$, and also to allow the stability analysis of any solution of (3.1). We require the solution to be defined on some interval $[0,T)$ where $0 < T < \infty$.

We further make the following assumptions --

A(i) The mutualist (u) can grow at low densities with or without the prey (x). This means that for u the mutualism is non-obligate. Mathematically

$$h(0,x) > 0, \quad \forall x.$$

A(ii) The mutualist (u) cannot multiply over a certain population size, which depends on the population size of its partner i.e. the prey (x). This means that the mutualist (u) has a carrying capacity, which is a function of the prey population. This puts the following restriction on $h(u,x)$

$$\exists L(x) \ni h(L(x),x) = 0 \quad \text{where} \quad L: R_+ \to R_+$$

We also assume that $\frac{dL}{dx} \geq 0$.

A(iii) Multiplication of the mutualist is slowed by an increase in their own numbers, other populations remaining the same i.e.

$$h_u(u,x) < 0.$$

This means that the mutualist exhibits density dependent growth.

A(iv) The multiplication of the mutualist is enhanced with an increase in the prey population, for any population of the mutualist. Mathematically

$$h_x(u,x) > 0.$$

This is the mutualistic effect.

A(v) The prey can grow at low densities with or without the presence of mutualist, so that mutualism for the prey is also non-obligate.

$$g(0,u) > 0, \quad \forall u.$$

A(vi) The environment has a carrying capacity for the prey, which depends on the population size of the mutualist, i.e.

$$\exists K(u) \ni g(K(u),u) = 0, \quad \text{where} \quad K: R_+ \to R_+ \text{ and } \frac{dK}{du} > 0.$$

A(vii) There may be a cost to x associating with the mutualist, i.e.

$$g_u(x,u) \leq 0.$$

A(viii) Multiplication of the prey is slowed down by an increase in their own number, for a fixed population size of the mutualist. Mathematically

$$g_x(x,u) < 0. \quad \text{(density dependent growth)}$$

A(ix) The predator functional response to prey density, which refers to the change in the density of prey attacked per unit of time per predator as the prey density changes, is assumed to be non-negative i.e.

$$p(x,u) \geq 0.$$

Also, there cannot be any predation in absence of prey, so we assume that $p(0,u) = 0$.

A(x) For fixed population sizes of other species, the predation is enhanced with the increase in number of the prey-species, that is

$$p_x(x,u) > 0.$$

A(xi) The mutualist cuts down the effectiveness of the predation on the prey. This translates into

$$p_u(x,u) \leq 0.$$

This is the main effect of the mutualist, incorporated in the model.

These assumptions are ecologically reasonable and are as exemplified in nature as mentioned in Chapter I. First we establish that the system (3.1) is well behaved in the sense that all the solutions remain bounded.

<u>Theorem 3.1</u>. Under the assumed mathematical restrictions on the

functions h, g and p, the solutions $u(t)$, $x(t)$ and $y(t)$ of (3.1) with positive initial conditions are all positive and bounded for $t \geq t_0$.

Proof: Let $u(t_0) = u_0$, $x(t_0) = x_0$ and $y(t_0) = y_0$ be the population sizes at time $t = t_0$, then we first prove that

$$x(t) \leq \max\{x_0, K(0)\} = M \quad \text{(say)}$$

Case (i) : Let $x_0 > K(0)$. Then we claim that $x(t) \leq x_0$ for $t \geq t_0$. Suppose this is not true then

$$\exists t_1 \geq t_0 \ni x(t_1) = x_0 \quad \text{and} \quad x'(t_1) \geq 0$$

But from (3.1)

$$\begin{aligned} x'(t_1) &= \alpha x(t_1) g(x(t_1), u(t_1)) - y(t_1) p(x(t_1), u(t_1)) \\ &= \alpha x_0 g(x_0, u(t_1)) - y(t_1) p(x_0, u(t_1)) \\ &< \alpha x_0 g(K(0), 0) - y(t_1) p(x_0, u(t_1)) \quad \text{(by A(vii), A(viii))} \\ &= 0 - y(t_1) p(x_0, u(t_1)). \quad \text{(by A(vi))} \end{aligned}$$

so that $x'(t) < 0$, contradiction.

Hence $x(t) \leq x_0$ for $t \geq t_0$.

Case (ii): Let $x_0 \leq K(0)$. Then we claim that $x(t) \leq K(0)$ for all $t \geq t_0$. Suppose this is not true then $\exists t_2 \geq t_0 \ni x(t_2) = K(0)$ and $x'(t_2) \geq 0$.

We consider two subcases.

Subcase (i): $x'(t_2) > 0$

From (3.1)

$$\begin{aligned} x'(t_2) &= \alpha x(t_2)g(x(t_2),u(t_2)) - y(t_2)P(x(t_2),u(t_2)) \\ &= \alpha K(0)g(K(0),u(t_2)) - y(t_2)P(K(0),u(t_2)) \\ &\leq \alpha K(0)g(K(0),0) \\ &= 0, \quad \text{condradiction.} \end{aligned}$$

Subcase (ii): $x'(t_2) = 0$

In this case if $y(t_2) > 0$ then we have as above

$$\begin{aligned} x'(t_2) &\leq \alpha K(0)g(K(0),0) - y(t_2)P(K(0),u(t_2)) \\ &< 0 \quad \text{contradiction.} \end{aligned}$$

If $y(t_2) = 0$ then again we can get contradiction if $g(K(0),u(t_2)) < g(K(0),0)$, so the only case left is when

$$y(t_2) = 0 \quad \text{and} \quad g(K(0),u(t_2)) = g(K(0),0).$$

In this case uniqueness of solutions to initial value problems imply that $x \equiv K(0)$ is a solution.

Thus we have proved that $x(t) \leq K(0)$. Combining results of the above two cases we have established that

$$x(t) \leq M \quad \text{for} \quad t \in [0,T).$$

Next we prove that

$$u(t) \leq \max\{u_0,L(M)\} = N \quad \text{(say)}.$$

Case (i): Let $u_0 > L(M)$. Then we claim that $u(t) \leq u_0$ for all $t \geq t_0$. Suppose this is not true then

$$\exists\, t_3 \geq t_0 \ni u(t_3) = u_0 \text{ and } u'(t_3) \geq 0.$$

But from (3.1)

$$\begin{aligned} u'(t_3) &= u(t_3)h(u(t_3),x(t_3)) \\ &= u_0 h(u_0,x(t_3)) \\ &< u_0 h(L(M),M) \quad \text{(by A(iii) and A(iv))} \\ &= 0 \quad \text{contradiction.} \end{aligned}$$

Hence $u(t) \leq u_0$ for $t \geq t_0$.

Case (ii): Let $u_0 \leq L(M)$. Then we claim that $u(t) \leq L(M)$, for all $t \geq t_0$. Suppose this is not true then

$$\exists\, t_4 \geq t_0 \ni u(t_4) = L(M) \text{ and } u'(t_4) \geq 0.$$

We consider two subcases.

Subcase (i): $u'(t_4) > 0$.

From (3.1)

$$\begin{aligned} u'(t_4) &= u(t_4)h(u(t_4),x(t_4)) \\ &= L(M)h(L(M),x(t_4)) \\ &\leq L(M)h(L(M),M) \\ &= 0, \quad \text{contradiction.} \end{aligned}$$

Subcase (ii): $u'(t_4) = 0$.

If $x(t_4) < M$ then again we will get contradiction because $u'(t_4) = L(M)h(L(M),x(t_4)) < L(M)h(L(M),M) = 0$ from A(iv).

So the only case left is when

$$u'(t_4) = 0, \quad h(L(M),x(t_4)) = h(L(M),M)$$

In this case uniqueness of solutions to initial value problems imply that

$$u \equiv L(M) \text{ is a solution.}$$

Hence in all cases $u(t) \leq L(M)$.

Now combining results of the above two cases we prove that

$$u(t) \leq N \quad \text{for} \quad t \in [0,T).$$

Finally we shall establish that $y(t)$ remains bounded. To prove this we consider

$$\begin{aligned} cx' + y' &= c[\alpha xg(x,u) - yp(x,u)] + y[-s+cp(x,u)] \\ &= c\alpha xg(x,u) - sy \\ &= c\alpha xg(x,u) + csx - s(cx+y) \\ &\leq A - s(cx+y) \end{aligned}$$

where $A = c\alpha Mg(0,0) + csM.$

Multiplying both sides of the above relation by e^{st} and rearranging we get

$$\frac{d}{dt}[(cx+y)e^{st}] \leq Ae^{st}.$$

From this, it follows that

$$[(cx+y)e^{st}]_{t_0}^{t} \leq \frac{A}{s}[e^{st}]_{t_0}^{t}$$

$$\text{or} \quad [cx(t)+y(t)]e^{st} - [cx_0+y_0]e^{st_0} \leq \frac{A}{s}[e^{st}-e^{st_0}].$$

Thus

$$[cx(t)+y(t)] \leq \frac{A}{s} + [cx_0+y_0 - \frac{A}{s}]e^{-s(t-t_0)}, \quad t \geq t_0$$

which gives that

$$[cx(t)+y(t)] \leq \max\{(cx_0+y_0), \frac{A}{s}\} \quad \text{for} \quad t \geq t_0.$$

Since $x(t)$ remains bounded, this inequality proves that $y(t)$ remains bounded for $t \geq t_0$. This completes the proof of the Theorem (3.1).

Note: Suppose that the assumption A(vii) is replaced by

$$g_u(x,u) \geq 0,$$

which is equivalent to u having a direct positive effect on x, then again we can get boundedness results if we make the following restriction on the function K,

$$\lim_{u\to\infty} K(u) = \tilde{K} < \infty.$$

3.2. Equilibrium States.

A set of solutions of system (3.1) is the set of stationary solutions for which the population growth of each species in the community is zero. The corresponding point in the phase space is known as the equilibrium point and the population sizes corresponding to this equilibrium point define the equilibrium state for the system (3.1).

E_1: $(0,0,0)$ is always an equilibrium state.

From A(ii) and A(vi), it is clear that

E_2: $(0,K(0),0)$ and

E_3: $(L(0),0,0)$ are also the equilibrium states.

If we assume that

$$\frac{s}{c} \in \text{Range } p(x,0) \tag{3.2}$$

and let $\hat{x}$ be such that

$$p(\hat{x},0) = \frac{s}{c} \tag{3.3}$$

then

E_4: $(0,\hat{x},\hat{y})$ is an equilibrium state, where

$$\hat{y} = \frac{\alpha\hat{x}g(\hat{x},0)}{p(\hat{x},0)} \tag{3.4}$$

In order to guarantee $\hat{y}$ positive, it is necessary to assume

$$\hat{x} < K(0) \tag{3.5}$$

Depending upon the number of intersections of the curves

$$u = L(x) \tag{3.6a}$$

$$x = K(u) \tag{3.6b}$$

we will have various equilibria in the u-x plane. After Rescigno and Richardson (1967), we can make some further assumptions on the functions h and g so as to guarantee the existence of a unique equilibrium interior to the u-x plane i.e.

E_5: $(\breve{u},\breve{x},0)$, where $\breve{u},\breve{x}$ are such that

$$L\big(K(\breve{u})\big) = \breve{u} \quad \text{and}$$

$$K\big(L(\breve{x})\big) = \breve{x}$$

Finally, we will write down conditions for there also to be an equilibrium interior to the first octant $(u>0,\ x>0,\ y>0)$. Any equilibrium of this type will be obtained by solving the following system of algebraic equations

$$h(u,x) = 0 \tag{3.7a}$$

$$\alpha x g(x,u) - y p(x,u) = 0 \tag{3.7b}$$

$$-s + c p(x,u) = 0 \tag{3.7c}$$

From (3.7a) we have $u = L(x)$, so that in order to solve for x by the equation (3.7c), we need to assume

$$\frac{s}{c} \in \text{Range } p(x,L(x)) \tag{3.8}$$

Under the assumption (3.8), the equation

$$-s + cp\bigl(x, L(x)\bigr) = 0 \tag{3.9}$$

can have several solutions, giving rise to several interior equilibria. The y-value of these equilibria is given by

$$y = \frac{\alpha x g(x,u)}{p(x,u)} \tag{3.10}$$

Again in order to guarantee a positive y-component, it is necessary to assume

$$x < K\bigl(L(x)\bigr) \tag{3.11}$$

To have a unique interior equilibrium, we further assume

$$p_x(x,u) + p_u L'(x) > 0 \tag{3.12}$$

Thus under the assumptions (3.8), (3.9), (3.11) and (3.12) there exists a unique interior equilibrium

E_6: (u^*, x^*, y^*), where

x^* is such that

$$p\bigl(x^*, L(x^*)\bigr) = \frac{s}{c} \tag{3.13a}$$

u^* is given by

$$u^* = L(x^*) \tag{3.13b}$$

and y^* is determined by

$$y^* = \frac{\alpha x^* g(x^*,u^*)}{p(x^*,u^*)} \tag{3.13c}$$

3.3. Stability of Equilibria.

The first objective in analyzing a model is to judge the stability of its equilibrium states. Depending upon whether the differential equations are assumed to apply over all conceivable combinations of population sizes or only in the neighbourhood of the equilibrium states, the stability analysis is referred to as global or local, respectively. The mathematical techniques have not yet been developed to perform the global analysis of a system like (3.1) in general. It has been observed that such systems can display a full and rich dynamical complexity such as the presence of strange attractors (May and Leonard, 1975). Such a complex behaviour is manifested even by the simple Lotka-Volterra equations for three competitors, which has been discussed by May and Leonard (1975). However, the local stability analysis can be done by computing the eigenvalues of the variational matrix at the equilibrium points.

The variational matrix for system (3.1) is given by

$$M(u,x,y) = \begin{bmatrix} h(u,x)+uh_u(u,x) & uh_x(u,x) & 0 \\ \alpha xg_u(x,u)-yp_u(x,u) & \alpha\big(g(x,u)+xg_x(x,u)\big)-yp_x(x,u) & -p(x,u) \\ cyp_u(x,u) & cyp_x(x,u) & -s+cp(x,u) \end{bmatrix} \tag{3.14}$$

Now we consider the various equilibrium states separately.

$E_1(0,0,0)$: From (3.14), we can compute the characteristic

equation for E_1. As mentioned in Chapter II, it is given by

$$\begin{vmatrix} h(0,0)-\lambda & 0 & 0 \\ 0 & \alpha g(0,0)-\lambda & 0 \\ 0 & 0 & -s-\lambda \end{vmatrix} = 0$$

The eigenvalues are $h(0,0)$, $\alpha g(0,0)$, $-s$. Since $h(0,0) > 0$ and $g(0,0) > 0$ from A(i) and A(v), the equilibrium state E_1 is unstable. Near E_1, the u and x populations grow whereas the y-population declines.

$E_2(0,K(0),0)$: The characteristic equation for E_2 is

$$\begin{vmatrix} h(0,K(0))-\lambda & 0 & 0 \\ \alpha K(0)g_u(K(0),0) & \alpha K(0)g_x(K(0),0)-\lambda & -p(K(0),0) \\ 0 & 0 & -s+cp(K(0),0)-\lambda \end{vmatrix} = 0$$

The eigenvalues are $h(0,K(0))$, $\alpha K(0)g_x(K(0),0)$ and $-s+cp(K(0),0)$. From the signs of these eigenvalues we conclude that E_2 is stable in the x-direction and unstable in the u- and y-directions. Here we have assumed that

$$p(K(0),0) > \frac{s}{c}. \tag{3.15}$$

This is reasonable to assume, biologically, because in the absence of the mutualist and when the prey population is near its carrying capacity, the predators must multiply.

$E_3(L(0),0,0)$: The variational matrix $M(u,x,y)$, evaluated at E_3, assumes the form

$$\begin{bmatrix} L(0)h_u(L(0),0) & L(0)h_x(L(0),0) & 0 \\ 0 & \alpha g(0,L(0)) & 0 \\ 0 & 0 & -s \end{bmatrix}$$

so that the eigenvalues are $L(0)h_u(L(0),0) < 0$, $\alpha g(0,L(0)) > 0$ and $-s < 0$. This means that E_3 attracts in the u-direction and y-direction but repels in the x-direction.

$E_4(0,\hat{x},\hat{y})$: This is an interior equilibrium for a predator-prey system, in the absence of the mutualist. We have a very rich literature to analyze such a system. Here we will mention a few results. The characteristic equation at E_4 is

$$\begin{vmatrix} h(0,\hat{x})-\lambda & 0 & 0 \\ \alpha\hat{x}g_u(\hat{x},0)-\hat{y}p_u(\hat{x},0) & \alpha(g(\hat{x},0)+\hat{x}g_x(\hat{x},0))-\hat{y}p_x(\hat{x},0)-\lambda & -p(\hat{x},0) \\ c\hat{y}p_u(\hat{x},0) & c\hat{y}p_x(\hat{x},0) & -\lambda \end{vmatrix} = 0$$

Expanding the determinant we get

$$[h(0,\hat{x})-\lambda][\lambda^2-\lambda\{\alpha g(\hat{x},0)+\alpha\hat{x}g_x(\hat{x},0)-\hat{y}p_x(\hat{x},0)\}+c\hat{y}p(\hat{x},0)p_x(\hat{x},0)] = 0.$$

If λ_1, λ_2 and λ_3 are roots of this equation then

$$\lambda_1 = h(0,\hat{x}) > 0$$

$$\lambda_2 + \lambda_3 = \alpha g(\hat{x},0) + \alpha\hat{x}g_x(\hat{x},0) - \hat{y}p_x(\hat{x},0) = H(\hat{x}) \quad \text{(say)}$$

$$\lambda_2\lambda_3 = c\hat{y}p(\hat{x},0)p_x(\hat{x},0) > 0$$

where $\quad H(\hat{x}) = \alpha g(\hat{x},0) + \alpha\hat{x}g_x(\hat{x},0) - \dfrac{\alpha\hat{x}g(\hat{x},0)}{p(\hat{x},0)} \cdot p_x(\hat{x},0)$ using (3.4)

or $$H(\hat{x}) = \alpha\hat{x}g(\hat{x},0)\, \frac{d}{dx}\, \ell n \left[\frac{xg(x,0)}{p(x,0)}\right]_{x=\hat{x}} \qquad (3.16a)$$

Since the product of the eigenvalues λ_2 and λ_3 is positive, the real parts of λ_2 and λ_3 have the same sign as $H(\hat{x})$.

$$\begin{aligned} &\text{If } H(\hat{x}) < 0, \quad E_4 \text{ is asymptotically stable} \\ &\quad\;\; H(\hat{x}) > 0, \quad E_4 \text{ is unstable} \end{aligned} \tag{3.16b}$$

in the xy plane. Freedman (1976) has given the graphical analysis of this case and accordingly, we can mention the following theorem for our system.

<u>Theorem 3.2</u>. If the assumptions of section A hold then at least one of the following is valid

(i) E_4 is asymptotically stable in the x-y plane but unstable in the u-direction.

(ii) The system (3.1) has a periodic solution surrounding E_4 in the x-y-plane and lying in the strip

$$\{(u,x,y) \mid u = 0, \quad 0<x<K(0), \quad y>0\}.$$

The periodic solution is stable from the outside in the plane but unstable in the u-direction.

$E_5(\breve{u},\breve{x},0)$: In the u-x plane, the system (3.1) assumes the form of a Kolmogorov-type growth model. Such a system has been analyzed by Rescigno and Richardson (1967) and Albrecht et al. (1974) in detail. The eigenvalues of the variational matrix at E_5 are the roots of the equation

$$[-s+cp(\tilde{x},\tilde{u})-\lambda][\lambda^2-\lambda\{\tilde{u}h_u(\tilde{u},\tilde{x})+\alpha\tilde{x}g_x(\tilde{x},\tilde{u})\}$$
$$+\alpha\tilde{u}\tilde{x}\{h_u(\tilde{u},\tilde{x})g_x(\tilde{x},\tilde{u})-h_x(\tilde{u},\tilde{x})g_u(\tilde{x},\tilde{u})\}] = 0$$

so that the roots $\lambda_1, \lambda_2, \lambda_3$ are given by

$$\lambda_3 = cp(\tilde{x},\tilde{u}) - s$$
$$\lambda_1 + \lambda_2 = \tilde{u}h_u(\tilde{u},\tilde{x}) + \alpha\tilde{x}g_x(\tilde{x},\tilde{u}) < 0$$
$$\lambda_1\lambda_2 = \alpha\tilde{u}\tilde{x}\{h_u(\tilde{u},\tilde{x})g_x(\tilde{x},\tilde{u})-h_x(\tilde{u},\tilde{x})g_u(\tilde{x},\tilde{u})\}$$
$$h_u(\tilde{u},\tilde{x}) < 0, \quad g_x(\tilde{x},\tilde{u}) < 0 \Rightarrow \lambda_1 + \lambda_2 < 0$$

Since $g_u(\tilde{x},\tilde{u}) \leq 0$, $\lambda_1 \cdot \lambda_2 > 0$, so that in this case E_5 is asymptotically stable in the u-x plane but the stability in the y-direction depends upon the sign of $\{p(\tilde{x},\tilde{u}) - \frac{s}{c}\}$.

Note: If we assume that the species u and x are mutualistic even in the absence of the predator i.e. if we assume that

$$g_u(x,u) > 0 \tag{3.17a}$$

and also make further assumptions

$$uh_u(u,x) + xh_x(x,u) \leq -\alpha < 0 \tag{3.17b}$$

$$ug_u(x,u) + xg_x(x,u) \leq -\alpha < 0, \tag{3.17c}$$

then again, we can have the same conclusion as before. Because (3.17b) and (3.17c) $\Rightarrow \left\{ \begin{array}{l} \tilde{x}h_x(\tilde{u},\tilde{x}) < -\tilde{u}h_u(\tilde{u},\tilde{x}) \\ \tilde{u}g_u(\tilde{x},\tilde{u}) < -\tilde{x}g_x(\tilde{x},\tilde{u}) \end{array} \right. \Rightarrow h_u(\tilde{u},\tilde{x})g_x(\tilde{x},\tilde{u}) - h_x(\tilde{u},\tilde{x})g_u(\tilde{x},\tilde{u})>0$

In biological terms, conditions (3.17b) and (3.17c) imply that for a

constant ratio $\frac{u}{x}$, the multiplication of each species is slowed by an increase in the number of individuals of both species.

At this point it will be shown that $(\tilde{u},\tilde{x},0)$ is stable in the large for solutions initiation in the u-x plane.

Theorem 3.3. Let $h(u,x)$ and $g(x,u)$ have the previously stated assumptions. Then $(\tilde{u},\tilde{x},0)$ is asymptotically stable in the large for solutions initiating in the positive quadrant of the u-x plane.

Proof: By Theorem 3.1, solutions initiating in R, remain in R, where $R = \{(u,x)\colon \varepsilon \leq u \leq \tilde{u} + a,\ \varepsilon \leq x \leq \tilde{x} + b,\ a > 0,\ b > 0,\ \varepsilon > 0\}$. Let $F(u,h) = uh(u,x)$ and $G(u,h) = \alpha x g(x,u)$ and $B(u,x) = u^{-1}x^{-1}$. Then

$$\frac{\partial}{\partial u}(BF) + \frac{\partial}{\partial x}(BG) = x^{-1}h_u(u,x) + \alpha u^{-1}g_x(x,u) \leq 0$$

and is not identically zero in R. Then by Dulac's Theorem there are no nontrivial periodic solutions in R. Hence the ω-limit set of all solutions initiating in R must be the point $(\tilde{u},\tilde{x},0)$. Q.E.D.

$E_6(u^*,x^*,y^*)$: Finally we compute the stability of the interior equilibrium. Using the relation (3.14), the variational matrix at E_6 assumes the form

$M(u^*,x^*,y^*) =$

$$\begin{bmatrix} u^*h_u(u^*,x^*) & u^*h_x(u^*,x^*) & 0 \\ \alpha x^*g_u(x^*,u^*)-y^*p_u(x^*,u^*) & \alpha\big(g(x^*,u^*)+x^*g_x(x^*,u^*)\big)-y^*p_x(x^*,u^*) & -p(x^*,u^*) \\ cy^*p_u(x^*,u^*) & cy^*p_x(x^*,u^*) & 0 \end{bmatrix}$$

The eigenvalues of this matrix are given by the equation

$$\lambda^3 - \{\alpha g(x^*,u^*)+\alpha x^*g_x(x^*,u^*)-y^*p_x(x^*,u^*)+u^*h_u(u^*,x^*)\}\lambda^2$$
$$+ [cy^*p(x^*,u^*)p_x(x^*,u^*)+u^*h_u(u^*,x^*)\{\alpha g(x^*,u^*)+\alpha x^*g_x(x^*,u^*)-y^*p_x(x^*,u^*)\}$$
$$+ u^*h_x(u^*,x^*)\{y^*p_u(x^*,u^*)-\alpha x^*g_u(x^*,u^*)\}]\lambda$$
$$- cu^*y^*p(x^*,u^*)\{h_u(u^*,x^*)p_x(x^*,u^*)-h_x(u^*,x^*)p_u(x^*,u^*)\} = 0$$

or
$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0 \qquad (3.18)$$

where

$$a_1 = -\left[\alpha g(x^*,u^*)\left\{1-\frac{cx^*p_x(x^*,u^*)}{s}\right\}+\alpha x^*g_x(x^*,u^*) + L(x^*)h_u(u^*,x^*)\right]$$

$$a_2 = \Big[\alpha g(x^*,u^*)\{cx^*p_x(x^*,u^*)+L(x^*)h_u(u^*,x^*)\} + \alpha x^*L(x^*)\{h_u(u^*,x^*)g_x(x^*,u^*)$$
$$-h_x(u^*,x^*)g_u(x^*,u^*)\} + \frac{c\alpha x^*L(x^*)g(x^*,u^*)}{s}\{h_x(u^*,x^*)p_u(x^*,u^*)$$
$$-h_u(u^*,x^*)p_x(x^*,u^*)\}\Big]$$

and

$$a_3 = -c\alpha x^*L(x^*)g(x^*,u^*)\{h_u(u^*,x^*)p_x(x^*,u^*)-h_x(u^*,x^*)p_u(x^*,u^*)\}$$

using the relations (3.13 a,b,c).

By the Routh-Hurwitz Criteria, the roots of equation (3.18) will have all negative real parts iff

$$a_1 > 0, \quad a_3 > 0 \quad \text{and} \quad a_1a_2 - a_3 > 0 \tag{3.19}$$

Here

$$\begin{aligned} a_1a_2-a_3 = {} & c\alpha x^*L(x^*)g(x^*,u^*)\left(\frac{a_1}{s} -1\right)\{h_x(u^*,x^*)p_u(x^*,u^*)-h_u(u^*,x^*)p_x(x^*,u^*)\} \\ & + \alpha a_1[g(x^*,u^*)\{cx^*p_x(x^*,u^*)+L(x^*)h_u(u^*,x^*)\} \\ & +x^*L(x^*)\{h_u(u^*,x^*)g_x(x^*,u^*)-h_x(u^*,x^*)g_u(x^*,u^*)\}] \end{aligned} \tag{3.20}$$

Hence we have

<u>Theorem 3.4</u>. Let the assumptions in Section A and the conditions (3.8), (3.9), (3.11) and (3.12) hold. Then there exists a unique interior equilibrium for system (3.1), which is asymptotically stable (locally) iff $a_1 > 0$, $a_3 > 0$ and $a_1a_2 - a_3 > 0$.

<u>Corollary 3.5</u>. The interior equilibrium (E_6) is asymptotically stable if the following conditions hold

(i) $a_1 > s$

(ii) $cx^*p_x(x^*,u^*) + u^*h_u(u^*,x^*) \geq 0$

(iii) $h_x(u^*,x^*)p_u(x^*,u^*) - h_u(u^*,x^*)p_x(x^*,u^*) > 0$

Proof: From (i) we get $a_1 > 0$, from (iii) we have $a_3 > 0$ and the conditions (ii) and (iii) guarantee that $a_1a_2 - a_3 > 0$. Hence by the Routh-Hurwitz criteria, the roots of the equation (3.18) have all negative real parts. This proves the Corollary using Theorem (3.4).

Example: Consider the following predator prey model

$$x' = x(1-x) - 2xy$$
$$y' = y(-1+2x)$$

The interior equilibrium can be shown to be $(\frac{1}{2}, \frac{1}{4})$. For the stability of this equilibrium, we can apply the criterion given in Freedman (1976). Here

$$g(x) = 1 - x, \quad p(x) = 2x, \quad s = 1, \quad x^* = \tfrac{1}{2}$$

$$\begin{aligned} H(x^*) &= x^*g_x(x^*) + g(x^*) - \frac{x^*g(x^*)p_x(x^*)}{p(x^*)} \\ &= \tfrac{1}{2}\cdot(-1) + (\tfrac{1}{2}) - \frac{\frac{1}{2}\cdot\frac{1}{2}\cdot 2}{1} \\ &= -\tfrac{1}{2} < 0 \end{aligned}$$

Hence the interior equilibrium is asymptotically stable. Now let us introduce the mutualist, whose effect is to cut down the predation. Consider the model

$$u' = u\left(1 - \frac{u}{1+\varepsilon x}\right)$$
$$x' = x(1-x) - \frac{2xy}{1+\delta u}$$

$$y' = u\left(-1 + \frac{2x}{1+\delta u}\right)$$

It can be shown that, if ε and δ are large enough e.g. $\varepsilon = \delta = 1$ (say) then the above system does not have an interior equilibrium but if ε and δ are small enough such that

$$1 - \delta - \varepsilon\delta > 0$$

then there exists an interior equilibrium

$$E = \left(\frac{2+\varepsilon}{2-\varepsilon\delta}, \quad \frac{1+\delta}{2-\varepsilon\delta}, \quad \frac{(1+\delta)(1-\delta-\varepsilon\delta)}{(2-\varepsilon\delta)^2}\right)$$

E satisfies all the conditions of Corollary (3.5) and hence the interior equilibrium is asymptotically stable.

3.4. Stability theorem according to the first approximation and the domain of asymptotic stability:

We make a change of variables in system (3.1) as follows

$$u - u^* = u_1 \tag{3.21a}$$

$$x - x^* = x_1 \tag{3.21b}$$

$$y - y^* = y_1 \tag{3.21c}$$

where (u^*,x^*,y^*) is the interior equilibrium of system (3.1). Now introducing

$$Z = (u_1,x_1,y_1)^T \quad \text{(Column vector)} \tag{3.22}$$

the system (3.1) can be represented in the form

$$Z' = AZ + F(Z) \tag{3.23a}$$

where $A =$

$$\begin{bmatrix} u^*h_u(u^*,x^*) & u^*h_x(u^*,x^*) & 0 \\ \alpha x^*g_u(x^*,u^*)-y^*p_u(x^*,u^*) & \alpha\big(g(x^*,u^*)+x^*g_x(x^*,u^*)\big)-y^*p_x(x^*,u^*) & -p(x^*,u^*) \\ cy^*p_u(x^*,u^*) & cy^*p_x(x^*,u^*) & 0 \end{bmatrix}$$

and $F(Z)$ is a column vector given by

$$F(Z) = \begin{bmatrix} F_1(u_1,x_1,y_1;\ u^*,x^*,y^*) \\ F_2(u_1,x_1,y_1;\ u^*,x^*,y^*) \\ F_3(u_1,x_1,y_1;\ u^*,x^*,y^*) \end{bmatrix} \tag{3.23b}$$

where $F_1(u_1,x_1,y_1;\ u^*,x^*,y^*) = (u_1+u^*)h(u_1+u^*,x_1+x^*) - u^*u_1h_u(u^*,x^*) - u^*x_1h_x(u^*,x^*)$

$$\begin{aligned} F_2(u_1,x_1,y_1;\ u^*,x^*,y^*) = {} & \alpha(x_1+x^*)g(x_1+x^*,u_1+u^*) - (y_1+y^*)p(x_1+x^*,u_1+u^*) \\ & - u_1\big(\alpha x^*g_u(x^*,u^*)-y^*p_u(x^*,u^*)\big) + y_1p(x^*,u^*) \\ & - x_1\{\alpha\big(g(x^*,u^*)+x^*g_x(x^*,u^*)\big)-y^*p_x(x^*,u^*)\} \end{aligned}$$

and

$$\begin{aligned} F_3(u_1,x_1,y_1;\ u^*,x^*,y^*) = {} & (y_1+y^*)\big(-s+cp(x_1+x^*,u_1+u^*)\big) \\ & -cy^*\big(u_1p_u(x^*,u^*)+x_1p_x(x^*,u^*)\big) \end{aligned}$$

The linear approximation of system (3.1) near the equilibrium state (u^*,x^*,y^*) is

$$Z' = AZ \tag{3.24}$$

Now we state the following theorem.

Theorem 3.6. Let the assumptions in Section A and conditions (3.8), (3.9), (3.11) and (3.12) hold, and let a_1, a_2, a_3 be as in (3.8). Also let

(i) $a_1 > 0$, $a_3 > 0$ and $a_1 a_2 - a_3 > 0$

(ii) $\lim_{\|Z\| \to 0} \left\{ \frac{\|F(Z)\|}{\|Z\|} \right\} = 0$

Then $Z(t) = 0$, $t \geq t_0$ for any $t_0 > 0$ is an asymptotically stable solution of (3.23)

Proof: We outline the proof, which is given in Jordan and Smith (1977) because from that we would be able to say something about the domain of asymptotic stability.

Due to condition (i), A is a stable matrix, so that there exist constants $c > 0$, $\gamma < 0$ such that

$$\| e^{At} \|, \quad \| e^{A^T t} \| \leq c e^{\gamma t} \qquad t \geq t_0 > 0 \tag{3.25}$$

We can construct a strong Liapunov function

$$V(Z) = Z^T K Z \tag{3.26A}$$

where

$$K = \int_0^\infty e^{A^T t} \cdot e^{At} dt. \tag{3.26B}$$

The condition (3.25) ensures the convergence of the above integral. $V(Z)$ is positive definite, which becomes obvious when we rewrite it in

the form

$$V(Z) = \int_0^\infty (e^{As}Z)^T (e^{As}Z)\,ds.$$

Here the integrand is simply the sum of certain squares. Now we compute the time derivative of $V(Z)$ along the solutions of (3.23), using the relation (3.26A).

$$\begin{aligned} \frac{dV\big(Z(t)\big)}{dt} &= (Z')^T KZ + Z^T KZ' \\ &= \big(AZ+F(Z)\big)^T KZ + Z^T K\, AZ+F(Z) \\ &= Z^T(A^T K+KA)Z + F^T(Z)KZ + Z^T KF(Z) \end{aligned} \qquad (3.27)$$

Now consider the product $(e^{A^T t} \cdot e^{At})$. We can write

$$\frac{d}{dt}\left(e^{A^T t} \cdot e^{At}\right) = A^T e^{A^T t} e^{At} + e^{A^T t} e^{At} \cdot A$$

Hence

$$\int_0^\infty \frac{d}{dt}\left(e^{A^T t} \cdot e^{At}\right)dt = A^T \int_0^\infty e^{A^T t} \cdot e^{At}\,dt + \left\{\int_0^\infty e^{A^T t} \cdot e^{At}\right\} A,$$

which gives

$$-I = A^T K + KA.$$

Using this relation, the equation (3.27) becomes

$$\frac{dV\big(Z(t)\big)}{dt} = -Z^T Z + 2F^T(Z)KZ$$

From $F(0) = 0$ (from 3.23b) and the condition (ii) we obtain that for a given $\varepsilon > 0 \; \exists \delta > 0 \ni \|Z\| < \delta \Rightarrow \|F(Z)\| < \varepsilon\|Z\|$. Using this we can show that

$$V'(Z) \leq -\|Z\|^2\{1-2\varepsilon\|K\|\}$$

Thus if $\varepsilon < \frac{1}{4\|K\|}$ then $V'(Z) < 0$ on $\|Z\| < \delta$ (3.28)

This proves that $Z(t) = 0$ is an asymptotically stable solution of (3.23).

Domain of asymptotic stability:

From the above proof it is apparent that it has not only been proved that the zero solution is asymptotically stable, but that all solutions starting in certain neighbourhoods of the origin are asymptotically stable. Such a neighbourhood determines the domain of asymptotic stability, with respect to the particular Liapunov function considered, so that this does not necessarily determine the largest domain. Now as mentioned in Chapter II, the domain of asymptotic stability $R(V:\varepsilon)$ will be taken to be the region in which $V(Z)$ and $(-V'(Z))$ have the property I. So that we can say that

$$R(V;\varepsilon) = \left\{ Z: Z \in J_\delta \cap \psi_{c_{max}} \right\}$$

where

$$J_\delta = \{Z: \|Z\| < \delta\}.$$

3.5. Periodic Solutions.

In this section we obtain the conditions on the parameters to guarantee the existence of small amplitude periodic solutions for the general system (3.1). As mentioned earlier in Section C, in stepping up to three dimensional models, numerous problems are encountered. Theorems like the Poincare-Bendixon Theorem do not hold for dimensions greater than two. In such a situation, the Hopf Bifurcation Theorem is one of the important direct tools, which helps us to establish the existence of the periodic solutions to non-linear systems of order greater than or equal to two. Experimentalists have shown that sometimes oscillations occur as a result of changing some condition or parameter in the environment (see Bünning 1973), so that theorems of the type mentioned in this section could be of great help in providing the mathematical description of these phenomena.

Let (u^*,x^*,y^*) be the interior equilibrium state for the system (3.1). The characteristic roots of the variational matrix evaluated at (u^*,x^*,y^*) are given by equation (3.18). Rewriting this equation we have

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0 \tag{3.29a}$$

where

$$a_1 = -[\alpha g(x^*,u^*)+\alpha x^* g_x(x^*,u^*)-y^* p_x(x^*,u^*)+u^* h_u(u^*,x^*)] \tag{3.29b}$$

$$\begin{aligned} a_2 = [&\alpha g(x^*,u^*)\big(cx^* p_x(x^*,u^*)+u^* h_u(u^*,x^*)\big) \\ &+\alpha u^* x^*\big(h_u(u^*,x^*)g_x(x^*,u^*)-h_x(u^*,x^*)g_u(x^*,u^*)\big) \\ &+u^* y^*\big(h_x(u^*,x^*)p_u(x^*,u^*)-h_u(u^*,x^*)p_x(x^*,u^*)\big)] \end{aligned} \tag{3.29c}$$

and

$$a_3 = -su^*y^*\big(h_u(u^*,x^*)p_x(x^*,u^*)-h_x(u^*,x^*)p_u(x^*,u^*)\big) \tag{3.29d}$$

We introduce two constants b_1 and b_2, which are given by

$$\begin{aligned} b_1 = \Bigg[&g(x^*,u^*)\left(\frac{cx^*p_x(x^*,u^*)}{s} - 1\right)-x^*g_x(x^*,u^*)\Bigg]\Bigg[g(x^*,u^*)\big(cx^*p_x(x^*,u^*) \\ &+u^*h_u(u^*,x^*)\big)+u^*x^*\big(h_u(u^*,x^*)g_x(x^*,u^*)-h_x(u^*,x^*)g_u(x^*,u^*)\big) \\ &+\frac{cu^*x^*g(x^*,u^*)}{s}\big(h_x(u^*,x^*)p_u(x^*,u^*)-h_u(u^*,x^*)p_x(x^*,u^*)\big)\Bigg] \end{aligned} \tag{3.30a}$$

$$\begin{aligned} b_2 = -u^*h_u(u^*,x^*)\Bigg[&g(x^*,u^*)\big(cx^*p_x(x^*,u^*)+u^*h_u(u^*,x^*)\big) \\ &+u^*x^*\big(h_u(u^*,x^*)g_x(x^*,u^*)-h_x(u^*,x^*)g_u(x^*,u^*)\big) \\ &+\frac{cu^*x^*g(x^*,u^*)}{s}\big(h_x(u^*,x^*)p_u(x^*,u^*)-h_u(u^*,x^*)p_x(x^*,u^*)\big)\Bigg] \\ &-cu^*x^*g(x^*,u^*)\big(h_x(u^*,x^*)p_u(x^*,u^*)-h_u(u^*,x^*)p_x(x^*,u^*)\big) \end{aligned} \tag{3.30b}$$

Now we state the following Hopf Bifurcation Theorem for the general model (3.1).

<u>Theorem 3.7</u>. Let (u^*,x^*,y^*) be the interior equilibrium state of the system (3.1). Further, let the following conditions hold

(i) $a_1,a_2,a_3 > 0$

(ii) $b_1b_2 < 0$.

Then, as the value of α (the bifurcation parameter) passes through $\alpha_0 \left(= -\frac{b_2}{b_1}\right)$, small amplitude periodic solutions of the system (3.1)

appear, which bifurcate from the equilibrium state (u^*,x^*,y^*). Here a_1,a_2,a_3 are given by (3.29) and b_1,b_2, by (3.30).

Proof: First we show that when $\alpha = \alpha_0$, the characteristic equation (3.29a) has one real and two pure imaginary roots. For this we compute $(a_1a_2-a_3)$ and express it as a polynomial in α. Using the relations (3.29b), (3.29c) and (3.29d) are also (3.13c), it can be shown that

$$\begin{aligned} a_1a_2-a_3 = &-\left[\alpha g(x^*,u^*)+\alpha x^* g_x(x^*,u^*)-\frac{\alpha x^* g(x^*,u^*)p_x(x^*,u^*)}{p(x^*,u^*)}+u^*h_u(u^*,x^*)\right] \\ &\cdot\Big[\alpha g(x^*,u^*)\big(cx^*p_x(x^*,u^*)+u^*h_u(u^*,x^*)\big) \\ &\quad +\alpha u^*x^*\big(h_u(u^*,x^*)g_x(x^*,u^*)-h_x(u^*,x^*)g_u(x^*,u^*)\big) \\ &\quad +\frac{\alpha x^*u^*g(x^*,u^*)}{p(x^*,u^*)}\big(h_x(u^*,x^*)p_u(x^*,u^*)-h_u(u^*,x^*)p_x(x^*,u^*)\big)\Big] \\ &+\frac{s\alpha x^*u^*g(x^*,u^*)}{p(x^*,u^*)}\big(h_u(u^*,x^*)p_x(x^*,u^*)-h_x(u^*,x^*)p_u(x^*,u^*)\big) \end{aligned}$$

Now using (3.13a), (3.30a) and (3.30b), the above expression can be rewritten as

$$a_1a_2 - a_3 = b_1\alpha^2 + b_2\alpha$$

Hence when $\alpha = \alpha_0$

$$(a_1a_2-a_3)_{\alpha=\alpha_0} = \alpha_0(b_1\alpha_0+b_2) = 0 \qquad (3.31)$$

The condition (i) together with the relation (3.31) guarantees that when $\alpha = \alpha_0$, the characteristic equation (3.29a) has one real (negative) and two pure imaginary roots.

Next we show that the eigenvalues cross the imaginary axis with non-zero speed at $\alpha = \alpha_0$. We can assume that for the values of α near α_0, the characteristic roots are of the form

$$\lambda_1 \pm i\lambda_2, \quad \lambda_3$$

where λ_1, λ_2 and λ_3 are real numbers. In view of this the characteristic equation will be

$$(\lambda-\lambda_3)[(\lambda-\lambda_1)^2+\lambda_2^2] = 0$$

or

$$\lambda^3 - (\lambda_3+2\lambda_1)\lambda^2 + (\lambda_1^2+\lambda_2^2+2\lambda_1\lambda_3)\lambda - (\lambda_1^2+\lambda_2^2)\lambda_3 = 0 \tag{3.32}$$

Now comparing (3.29a) and (3.32), we get

$$a_1 = -(\lambda_3+2\lambda_1) \tag{3.33a}$$

$$a_2 = \lambda_1^2 + \lambda_2^2 + 2\lambda_1\lambda_3 \tag{3.33b}$$

$$a_3 = -(\lambda_1^2+\lambda_2^2)\lambda_3 \tag{3.33c}$$

From (3.33a) $\qquad \lambda_3 = -a_1 - 2\lambda_1 \qquad (3.34)$

From (3.33b) $\qquad a_2\lambda_3 = \lambda_3(\lambda_1^2+\lambda_2^2) + 2\lambda_1\lambda_3^2$

or $\qquad a_2\lambda_3 = -a_3 + 2\lambda_1\lambda_3^2 \qquad$ from (3.33c)

or $\qquad a_2(-a_1-2\lambda_1) = -a_3 + 2\lambda_1(a_1+2\lambda_1)^2 \qquad$ using (3.34)

so that $\qquad a_2(a_1+2\lambda_1) = a_3 - 2\lambda_1(a_1+2\lambda_1)^2 \qquad (3.35)$

Now let us differentiate this relation with respect to the parameter α throughout. We get

$$\frac{da_2}{d\alpha}(a_1+2\lambda_1) + a_2\left(\frac{da_1}{d\alpha} + 2\frac{d\lambda_1}{d\alpha}\right) = \frac{da_3}{d\alpha} - 2\frac{d\lambda_1}{d\alpha}(a_1+2\lambda_1)^2$$

$$- 2\lambda_1 \cdot 2(a_1+2\lambda_1)\cdot\left(\frac{da_1}{d\alpha} + 2\frac{d\lambda_1}{d\alpha}\right) \tag{3.36}$$

Now consider the equation (3.36) for $\alpha = \alpha_0$. Since we know that at $\alpha = \alpha_0$, two roots are pure imaginary,

$$(\lambda_1)_{\alpha=\alpha_0} = 0, \tag{3.37}$$

we get

$$\left[a_1\frac{da_2}{d\alpha} + a_2\frac{da_1}{d\alpha} - \frac{da_3}{d\alpha}\right]_{\alpha=\alpha_0} = -2\left[\frac{d\lambda_1}{d\alpha}(a_2+a_1^2)\right]_{\alpha=\alpha_0}$$

or
$$\left[\frac{d}{d\alpha}(a_1a_2-a_3)\right]_{\alpha=\alpha_0} = -2\left[\frac{d\lambda_1}{d\alpha}(a_1^2+a_2)\right]_{\alpha=\alpha_0}$$

or
$$[2b_1\alpha+b_2]_{\alpha=\alpha_0} = -2\left[\frac{d\lambda_1}{d\alpha}(a_1^2+a_2)\right]_{\alpha=\alpha_0}$$

Hence
$$\left.\frac{d\lambda_1}{d\alpha}\right|_{\alpha=\alpha_0} = -\frac{b_1\alpha_0}{2}\left[\frac{1}{a_1^2+a_2}\right]_{\alpha=\alpha_0} \neq 0 \tag{3.38}$$

This shows that the eigenvalues cross the imaginary axis, transversally, i.e. with non-zero speed.

Now the application of the Hopf Bifurcation Theorem, given in Chapter II, proves the theorem.

3.6. A Special Case.

In this section we analyze a special case of the general model (3.1), incorporating all its important features, as mentioned in Section A. We consider the following model

$$\left.\begin{aligned} u' &= \gamma u\left(1 - \frac{u}{L_0+\ell x}\right) \\ x' &= \alpha x\left(1 - \frac{x}{K}\right) - \frac{\beta xy}{1+mu} \\ y' &= y\left(-s + \frac{c\beta x}{1+mu}\right) \end{aligned}\right\} \tag{3.39}$$

where the parameters $\alpha,\beta,\gamma,\ell,L_0,K,m,c,s$ are all positive. This particular model refers to the case, where in the absence of the predator (y), the association between u and x is not mutualistic but commensal. The mutualism occurs when we introduce the predator into the system.

The interior equilibrium is obtained by solving the following system of algebraic equations

$$\begin{aligned} u &= L_0 + \ell x \\ \alpha\left(1 - \frac{x}{K}\right) &= \frac{\beta y}{1+mu} \\ s(1+mu) &= c\beta x \end{aligned}$$

From the first and the third of these we get

$$c\beta u - c\beta L_0 = c\beta\ell x = \ell s(1+mu)$$

or
$$u = \frac{\ell s + c\beta L_0}{c\beta - \ell ms}$$

Putting this value of u in the first equation; we get

$$x = \frac{s(1+mL_0)}{c\beta - \ell ms},$$

and then finally from the middle equation we solve for y:

$$y = \frac{1+mu}{\beta} \cdot \alpha \cdot \left(1 - \frac{x}{K}\right)$$

We denote the interior equilibrium by $E^*(u^*,x^*,y^*)$, where

$$\begin{aligned} u^* &= L_0 + \frac{\ell s}{c\beta}\lambda \\ x^* &= \frac{s\lambda}{c\beta} \\ y^* &= \frac{\alpha}{\beta} \cdot \lambda \left(1 - \frac{s\lambda}{c\beta K}\right), \end{aligned} \tag{3.40}$$

where

$$\lambda = \frac{c\beta(1+mL_0)}{c\beta - \ell ms} \tag{3.41}$$

To make the equilibrium E^* feasible, (i.e. positive), we assume

$$c\beta > \ell ms \tag{3.42a}$$

and $$1 - \frac{s\lambda}{c\beta K} > 0 \tag{3.42b}$$

The latter condition requires that $x^* < K$, which is the usual assumption in two-dimensional predator-prey systems.

Other equilibrium states are:

E_1: $(0,0,0)$

E_2: $(0,K,0)$

E_3: $(L_0,0,0)$

E_4: $\left(0, \frac{s}{c\beta}, \frac{\alpha}{\beta}(1 - \frac{s}{Kc\beta})\right)$

E_5: $(L_0+\ell K, K, 0)$

We will concentrate on the interior equilibrium E^* only. The variational matrix for system (3.39) is

$$M(u,x,y) = \begin{bmatrix} \gamma - \frac{2\gamma u}{L_0+\ell x} & \frac{\gamma \ell u^2}{(L_0+\ell x)^2} & 0 \\ \frac{\beta m x y}{(1+mu)^2} & \alpha - \frac{2\alpha x}{K} - \frac{\beta y}{1+mu} & \frac{-\beta x}{1+mu} \\ \frac{-c\beta m x y}{(1+mu)^2} & \frac{c\beta y}{(1+mu)} & -s + \frac{c\beta x}{(1+mu)} \end{bmatrix}$$

When evaluated at $E^*(u^*,x^*,y^*)$, using (3.40), we get

$$M(u^*,x^*,y^*) = \begin{bmatrix} -\gamma & \gamma\ell & 0 \\ \frac{ms\alpha}{c\beta}(1 - \frac{s\lambda}{c\beta K}) & -\frac{\alpha s\lambda}{c\beta K} & -\frac{s}{c} \\ -\frac{ms\alpha}{\beta}(1 - \frac{s\lambda}{c\beta K}) & \alpha c(1 - \frac{s\lambda}{c\beta K}) & 0 \end{bmatrix} \tag{3.43}$$

The eigenvalues of this matrix are given by the roots of the following cubic

$$\mu^3 + a_1\mu^2 + a_2\mu + a_3 = 0 \tag{3.44a}$$

where

$$a_1 = \gamma + \frac{\alpha s\lambda}{c\beta K} \tag{3.44b}$$

$$a_2 = (1 - \frac{s\lambda}{c\beta K})(1 - \frac{\gamma\ell m}{c\beta})\alpha s + \frac{\alpha s\gamma\lambda}{c\beta K} \tag{3.44c}$$

$$a_3 = \frac{\alpha s\gamma}{c\beta}(1 - \frac{s\lambda}{c\beta K})(c\beta - \ell ms) \tag{3.44d}$$

Clearly $a_1 > 0$ and from (3.42) $a_3 > 0$. Hence the roots of equation (3.44a) will have all negative real parts iff

$$a_1a_2 - a_3 > 0$$

or $$(\gamma + \frac{\alpha s\lambda}{c\beta K})\left[(1 - \frac{s\lambda}{c\beta K})(1 - \frac{\gamma\ell m}{c\beta})\alpha s + \frac{\alpha s\gamma\lambda}{c\beta K}\right] - \frac{\alpha s\gamma}{c\beta}(1 - \frac{s\lambda}{c\beta K})(c\beta - \ell ms) > 0$$

or $$\left[(1 - \frac{s\lambda}{c\beta K})(1 - \frac{\gamma\ell m}{c\beta})\alpha s + \frac{\alpha s\gamma\lambda}{c\beta K}\right] + (s-\gamma)(1 - \frac{s\lambda}{c\beta K})\frac{\gamma\ell mK}{\lambda} + \gamma^2 > 0 \tag{3.45}$$

The above discussion, proves the following result.

<u>Theorem 3.8</u>. Let the conditions (3.42a) and (3.42b) hold. Then there exists an interior equilibrium of the system (3.39), which is asymptotically stable (locally) if the parameters $\alpha,\beta,\gamma,\ell,L_0,K,m,c,s$ satisfy the inequality (3.45).

<u>Corollary 3.9</u>. Let the conditions

(i) $\ell m\gamma \leq \ell ms < c\beta$

(ii) $s\lambda < c\beta K$, where λ is given by (3.41) hold. Then there exists a unique interior equilibrium E^* of the system (3.39), which is asymptotically stable.

Proof: The conditions $\ell ms < c\beta$, $s\lambda < c\beta K$ guarantee the existence of the interior equilibrium E^*, as given by (3.40). From (i) we have $\frac{\ell m\gamma}{c\beta} \leq \frac{\ell ms}{c\beta} < 1$ and $\gamma \leq s$ this implies that $(1 - \frac{\gamma\ell m}{c\beta}) > 0$. From (ii) we have $(1 - \frac{s\lambda}{c\beta K}) > 0$. Now $(1 - \frac{s\lambda}{c\beta K}) > 0$, $(1 - \frac{\gamma\ell m}{c\beta}) > 0$ and $s \geq \gamma$ imply that the condition (3.45) is fulfilled. Hence the characteristic roots of the variational matrix for the system (3.39) at E^* have all negative real parts. This proves the corollary.

F_1. In this section we estimate an existence region of asymptotic stability by computing a strong Liapunov function for the corresponding linear approximation of the system (3.39) near E^*. First we shift the origin to (u^*,x^*,y^*) by the transformation

$$u - u^* = u_1$$

$$x - x^* = x_1$$

$$y - y^* = y_1$$

Under this transformation, the system (3.39) transforms to

$$u_1' = -\gamma u_1 + \gamma\ell x_1 - \frac{\gamma(\ell x_1 - u_1)^2}{u^* + \ell x_1}$$

$$x_1' = \frac{ms\alpha}{c\beta}(1 - \frac{x^*}{K})u_1 - \frac{\alpha x^*}{K}x_1 - \frac{s}{c}y_1$$

$$+ \frac{1}{c\beta K(1+mu^*+mu_1)}\Big[msK\beta u_1 y_1 - \alpha sm^2(K-x^*)u_1^2 - cK\beta^2 x_1 y_1 - m\alpha\beta c(K-x^*)u_1 x_1$$
$$- m\alpha\beta c u_1 x_1^2 - (1+mu^*)x_1^2\Big]$$

and

$$y_1' = -\frac{ms\alpha}{\beta}(1-\frac{x^*}{K})u_1 + c\alpha(1-\frac{x^*}{K})x_1 + \frac{1}{\beta K(1+mu^*+mu_1)}[\alpha sm^2(K-x^*)u_1^2$$
$$-m\alpha\beta c(K-x^*)u_1x_1 + cK\beta^2x_1y_1 - ms\beta Ku_1y_1]$$

Here u^*,x^*,y^* are known in terms of the parameters and are given by (3.40). Now let us introduce the column vector

$$Z = (u_1,x_1,y_1)^T$$

Using this the above system can be rewritten in the form

$$Z' = AZ + F(Z) \tag{3.46}$$

where A is a 3×3 matrix given by

$$A = \begin{bmatrix} -\gamma & \gamma\ell & 0 \\ \frac{ms\alpha}{c\beta}(1-\frac{x^*}{K}) & -\frac{\alpha x^*}{K} & -\frac{s}{c} \\ -\frac{ms\alpha}{\beta}(1-\frac{x^*}{K}) & c\alpha(1-\frac{x^*}{K}) & 0 \end{bmatrix}$$

and $F(Z)$ is a column vector given by

$$F(Z) = [F_1(u_1,x_1,y_1),F_2(u_1,x_1,y_1),F_3(u_1,x_1,y_1)]^T \tag{3.48}$$

where

$$F_1(u_1,x_1,y_1) = \frac{-\gamma(\ell x_1-u_1)^2}{u^*+\ell x_1}$$

$$F_2(u_1,x_1,y_1) = \frac{1}{c\beta K(1+mu^*+mu)}[msK\beta u_1y_1 - \alpha sm^2(K-x^*)u_1^2$$
$$-cK\beta^2x_1y_1 - m\alpha\beta c(K-x^*)u_1x_1 - m\alpha\beta cu_1x_1^2 - (1+mu^*)x_1^2]$$

$$F_3(u_1,x_1,y_1) = \frac{1}{\beta K(1+mu^*+mu_1)} [\alpha sm^2(K-x^*)u_1^2 - m\alpha\beta c(K-x^*)u_1x_1$$
$$+cK\beta^2 x_1y_1 - ms\beta Ku_1y_1]$$

The linear approximation of the system (3.39) near E^* is

$$Z' = AZ \tag{3.49}$$

As discussed earlier A is a stable matrix if the condition (3.45) is satisfied.

Liapunov function: If $Z(t) = 0$ is asymptotically stable then according to the standard ODE theory there exists a Liapunov function for (3.49). The Liapunov function can be taken in the form

$$V(Z) = Z^T BZ \tag{3.49}$$

where B is a 3×3 symmetric matrix (i.e. $B^T=B$), which satisfies the matrix equation

$$A^T B + BA = -I \tag{3.50}$$

In general the right hand side of the above equation is taken to be any negative definite and symmetric matrix. Let us denote

$$A = (a_{ij}), \quad B = (b_{ij}) \quad i,j = 1,2,3 \tag{3.51}$$

where

$$\left.\begin{array}{lll} a_{11} = -\gamma\ , & a_{12} = \gamma\ell, & a_{13} = 0 \\ a_{21} = \frac{ms\alpha}{c\beta}\left(1 - \frac{x^*}{K}\right) = \frac{ms}{c\lambda}\, y^*, & a_{22} = -\frac{\alpha x^*}{K}\ , & a_{23} = -\frac{s}{c} \\ a_{31} = -\frac{ms}{\lambda}\, y^*, & a_{32} = \frac{c\beta}{\lambda}\, y^*, & a_{33} = 0 \end{array}\right\} \qquad (3.52)$$

Equation (3.50), then becomes

$$\begin{bmatrix} a_{11} & a_{21} & a_{31} \\ a_{12} & a_{22} & a_{32} \\ a_{13} & a_{23} & a_{33} \end{bmatrix}\begin{bmatrix} b_{11} & b_{12} & b_{13} \\ b_{12} & b_{22} & b_{23} \\ b_{13} & b_{23} & b_{33} \end{bmatrix} + \begin{bmatrix} b_{11} & b_{12} & b_{13} \\ b_{12} & b_{22} & b_{23} \\ b_{13} & b_{23} & b_{33} \end{bmatrix}\begin{bmatrix} a_{11} & a_{12} & a_{13} \\ a_{21} & a_{22} & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix}$$

$$= \begin{bmatrix} -1 & 0 & 0 \\ 0 & -1 & 0 \\ 0 & 0 & -1 \end{bmatrix}$$

or

$$\left.\begin{array}{r} 2a_{11}b_{11} + 2a_{21}b_{12} + 2a_{31}b_{13} = -1 \\ 2a_{12}b_{12} + 2a_{22}b_{22} + 2a_{32}b_{23} = -1 \\ 2a_{23}b_{23} = -1 \\ a_{12}b_{11} + (a_{11}+a_{22})b_{12} + a_{21}b_{22} + a_{32}b_{13} + a_{31}b_{23} = 0 \\ a_{23}b_{21} + a_{11}b_{13} + a_{21}b_{23} + a_{31}b_{33} = 0 \\ a_{23}b_{22} + a_{22}b_{23} + a_{12}b_{13} + a_{32}b_{33} = 0 \end{array}\right\} \qquad (3.53)$$

From the third of equations (3.53)

$$b_{23} = -\frac{1}{2a_{23}} = \frac{c}{2s} \qquad (3.54)$$

The other elements of the matrix B i.e. $b_{11}, b_{12}, b_{13}, b_{22}, b_{33}$ are given by the following system of equations

$$
\begin{aligned}
(2a_{11})b_{11} + (2a_{21})b_{12} + (2a_{31})b_{13} + (0)b_{22} + (0)b_{33} &= -1 \\
(0)b_{11} + (2a_{12})b_{12} + (0)b_{13} + (2a_{22})b_{22} + (0)b_{33} &= -1 - 2a_{32}\cdot b_{23} \\
(a_{12})b_{11} + (a_{11}+a_{22})b_{12} + (a_{32})b_{13} + (a_{21})b_{22} + (0)b_{33} &= -a_{31}\cdot b_{23} \\
(0)b_{11} + (a_{23})b_{12} + (a_{11})b_{13} + (0)b_{22} + (a_{31})b_{33} &= -a_{21}b_{23} \\
(0)b_{11} + (0)b_{12} + (a_{12})b_{13} + (a_{23})b_{22} + (a_{32})b_{33} &= -a_{22}\cdot b_{23}
\end{aligned}
\tag{3.55}
$$

Using the Cramer's rule, we can solve the above system if the determinant of the coefficient matrix is non-zero. We show that the determinant of the coefficient matrix, denoted by Δ , is non-zero by evaluating

$$
\Delta = \begin{vmatrix}
2a_{11} & 2a_{21} & 2a_{31} & 0 & 0 \\
0 & 2a_{12} & 0 & 2a_{22} & 0 \\
a_{12} & a_{11}+a_{22} & a_{32} & a_{21} & 0 \\
0 & a_{23} & a_{11} & 0 & a_{31} \\
0 & 0 & a_{12} & a_{23} & a_{32}
\end{vmatrix}
$$

From (3.52), since $\ell a_{11} + a_{12} = 0$, we can write

$$
\Delta = 4\begin{vmatrix}
a_{11} & a_{21} & a_{31} & 0 & 0 \\
0 & a_{12} & 0 & a_{22} & 0 \\
0 & a_{11}+a_{22}+\ell a_{21} & a_{32}+\ell a_{31} & a_{21} & 0 \\
0 & a_{23} & a_{11} & 0 & a_{31} \\
0 & 0 & a_{12} & a_{23} & a_{32}
\end{vmatrix}
$$

or

$$
\Delta = 4a_{11}\begin{vmatrix}
a_{12} & 0 & a_{22} & 0 \\
a_{11}+a_{22}+\ell a_{21} & a_{32}+\ell a_{31} & a_{21} & 0 \\
a_{23} & a_{11} & 0 & a_{31} \\
0 & a_{12} & a_{23} & a_{32}
\end{vmatrix}
$$

From (3.52) $msa_{32} + c\beta a_{31} = 0$, so that

$$\Delta = \frac{4a_{11}}{msc\beta} \begin{vmatrix} a_{12} & 0 & a_{22} & 0 \\ a_{11}+a_{22}+\ell a_{21} & a_{32}+\ell a_{31} & a_{21} & 0 \\ c\beta a_{23} & c\beta a_{11}+msa_{12} & msa_{23} & 0 \\ 0 & a_{12} & a_{23} & a_{32} \end{vmatrix}$$

or

$$\Delta = \frac{4a_{11}a_{32}}{msc\beta} \begin{vmatrix} a_{12} & 0 & a_{22} \\ a_{11}+a_{22}+\ell a_{21} & a_{32}+\ell a_{31} & a_{21} \\ c\beta a_{23} & c\beta a_{11}+msa_{12} & msa_{23} \end{vmatrix}$$

Again from (3.52), since

$$\ell a_{31} + a_{32} = \frac{y^*}{\lambda} \cdot (c\beta-\ell ms)$$

$$c\beta a_{11} + msa_{12} = -\gamma(c\beta-\ell ms)$$

we get

$$\Delta = \frac{4a_{11}a_{32}(c\beta-\ell ms)}{c\beta ms} \begin{vmatrix} a_{12} & 0 & a_{22} \\ a_{11}+a_{22}+\ell a_{21} & \frac{y^*}{\lambda} & a_{21} \\ c\beta a_{23} & -\gamma & msa_{23} \end{vmatrix}$$

or

$$\Delta = \frac{4a_{11}a_{32}(c\beta-\ell ms)}{c\beta ms} \left[a_{12}\left(ms\ \frac{y^*}{\lambda}\ a_{23}+\gamma a_{21}\right)+a_{22}\left(-\gamma(a_{11}+a_{22}+\ell a_{21})-c\beta a_{23}\cdot\frac{y^*}{\lambda}\right)\right]$$

Using (3.52) and rearranging, we can show that

$$\Delta = \frac{4\gamma\alpha y^*(c\beta-\ell ms)}{c\beta mK}\left[(1-\frac{x^*}{K})(1-\frac{\gamma\ell m}{c\beta})\alpha s+\frac{\alpha\gamma s\lambda}{c\beta K}+(1-\frac{x^*}{K})(s-\gamma)\ \frac{\gamma\ell mK}{\lambda}+\gamma^2\right] \tag{3.56}$$

Since we have assumed that the real parts of the eigenvalues of all the roots of the matrix A are negative, the condition (3.45) is satisfied and hence

$$\Delta > 0 \tag{3.57}$$

Thus we can solve for $b_{11}, b_{12}, b_{13}, b_{22}, b_{33}$ from (3.55), using Cramer's Rule

$$b_{11} = \frac{1}{\Delta}\begin{vmatrix} -1 & 2a_{21} & 2a_{31} & 0 & 0 \\ -1-\frac{ca_{32}}{s} & 2a_{12} & 0 & 2a_{22} & 0 \\ -\frac{ca_{31}}{2s} & a_{11}+a_{22} & a_{32} & a_{21} & 0 \\ -\frac{ca_{21}}{2s} & a_{23} & a_{11} & 0 & a_{31} \\ -\frac{ca_{22}}{2s} & 0 & a_{12} & a_{23} & a_{32} \end{vmatrix} \tag{3.58a}$$

$$b_{12} = \frac{1}{\Delta}\begin{vmatrix} 2a_{11} & -1 & 2a_{31} & 0 & 0 \\ 0 & -1-\frac{ca_{32}}{s} & 0 & 2a_{22} & 0 \\ a_{12} & -\frac{ca_{31}}{2s} & a_{32} & a_{21} & 0 \\ 0 & -\frac{ca_{21}}{2s} & a_{11} & 0 & a_{31} \\ 0 & -\frac{ca_{22}}{2s} & a_{12} & a_{23} & a_{32} \end{vmatrix} \tag{3.58b}$$

$$b_{13} = \frac{1}{\Delta} \begin{vmatrix} 2a_{11} & 2a_{21} & -1 & 0 & 0 \\ 0 & 2a_{12} & -1-\frac{ca_{32}}{s} & 2a_{22} & 0 \\ a_{12} & a_{11}+a_{22} & -\frac{ca_{31}}{2s} & a_{21} & 0 \\ 0 & a_{23} & -\frac{ca_{21}}{2s} & 0 & a_{31} \\ 0 & 0 & -\frac{ca_{22}}{2s} & a_{23} & a_{32} \end{vmatrix} \qquad (3.58c)$$

$$b_{22} = \frac{1}{\Delta} \begin{vmatrix} 2a_{11} & 2a_{21} & 2a_{31} & -1 & 0 \\ 0 & 2a_{12} & 0 & -1-\frac{ca_{32}}{s} & 0 \\ a_{12} & a_{11}+a_{22} & a_{32} & -\frac{ca_{31}}{2s} & 0 \\ 0 & a_{23} & a_{11} & -\frac{ca_{21}}{2s} & a_{31} \\ 0 & 0 & a_{12} & -\frac{ca_{22}}{2s} & a_{32} \end{vmatrix} \qquad (3.58d)$$

$$b_{33} = \frac{1}{\Delta} \begin{vmatrix} 2a_{11} & 2a_{21} & 2a_{31} & 0 & -1 \\ 0 & 2a_{12} & 0 & 2a_{22} & -1-\frac{ca_{32}}{s} \\ a_{12} & a_{11}+a_{22} & a_{32} & a_{21} & -\frac{ca_{31}}{2s} \\ 0 & a_{23} & a_{11} & 0 & -\frac{ca_{21}}{2s} \\ 0 & 0 & a_{12} & a_{23} & -\frac{ca_{22}}{2s} \end{vmatrix} \qquad (3.58e)$$

Thus, the relations (3.52), (3.54), (3.56), (3.58a,b,c,d,e) determine the matrix B completely in terms of the parameters of the system (3.39).

The function $V(Z)$, then can be expressed as

$$V(Z) = b_{11}u_1^2 + b_{22}x_1^2 + b_{33}y_1^2 + 2b_{12}u_1x_1 + 2b_{23}x_1y_1 + 2b_{13}u_1y_1 \quad (3.59)$$

We prove the following result (E.A. Barbashin 1970)

Theorem 3.10. Suppose that

(i) the parameters $\alpha, \beta, \gamma \ldots$ satisfy the conditions (3.42), (3.45)

(ii) ρ^2 is the largest eigenvalue of the quadratic form

$$\left[\left(\frac{\partial V}{\partial u_1}\right)^2 + \left(\frac{\partial V}{\partial x_1}\right)^2 + \left(\frac{\partial V}{\partial y_1}\right)^2\right]$$

(iii) $\|Z(t)\| \leq k$, $t \geq t_0$ for any t_0 and $\frac{\rho \|F(Z)\|}{\|Z\|} < 1.$

Then $Z(t) = 0$ is an asymptotically stable solution of (3.46) and the part of the ball $\|Z\| < k$ in which $V(Z)$ has the property I is a domain of asymptotic stability with respect to the Liapunov function $V(Z)$.

Proof: Computing the derivative of $V(Z)$ along the solutions of (3.46) we get (Barbashin 1970)

$$V'(Z) = -\|Z\|^2 + \left(\frac{\partial V(Z)}{\partial u_1} F_1(Z) + \frac{\partial V(Z)}{\partial x_1} F_2(Z) + \frac{\partial V(Z)}{\partial y_1} F_3(Z)\right)$$

$$\leq -\|Z\|^2 + \left[\left(\frac{\partial V(Z)}{\partial u_1}\right)^2 + \left(\frac{\partial V(Z)}{\partial x_1}\right)^2 + \left(\frac{\partial V(Z)}{\partial y_1}\right)^2\right]^{\frac{1}{2}} \|F(Z)\|$$

using Schwarz inequality

$$\leq -\|Z\|^2 + \rho\|Z\| \, \|F(Z)\|$$

$$= -\|Z\|^2 \left[1 - \frac{\rho\|F(Z)\|}{\|Z\|}\right]$$

$< 0 \Rightarrow Z(t) = 0$ is asymptotically stable.

Since $V'(Z) < 0$ in $\|Z\| < k$, $\{-V'(Z)\}$ has the property I in $\|Z\| < k$. The interior of the ball $\|Z\| < k$ in which $V(Z)$ has the property I, will then determine the region of asymptotic stability. This domain of asymptotic stability depends upon the particular Liapunov function chosen and hence does not determine the largest such domain.

This proves the theorem.

Theorem 3.11. (A Bifurcation Theorem). Let the parameters $\alpha,\beta,\gamma,\ell,L_0$, K,m,c,s, all positive be such that

(i) $c\beta - \ell ms > 0$

(ii) $\left(\frac{c\beta+\ell ms}{c\beta\ell m}\right) \lambda < K$

(iii) $s \left[\frac{(1 - \frac{s\lambda}{c\beta K})}{1 - \frac{\lambda}{K}(\frac{c\beta+\ell ms}{c\beta\ell m})}\right] < \gamma < \frac{c\beta}{\ell m}\left[\frac{(1 - \frac{s\lambda}{c\beta K})}{1 - \frac{\lambda}{K}(\frac{c\beta+\ell ms}{c\beta\ell m})}\right]$

(iv) $\alpha_0 \equiv \dfrac{(1 - \frac{s\lambda}{c\beta K})(\gamma-s)\,\frac{\gamma\ell mK}{\lambda} - \gamma^2}{(1 - \frac{s\lambda}{c\beta K})(1 - \frac{\gamma\ell m}{c\beta})s + \frac{\gamma s\lambda}{c\beta K}} \in$ range of values of α

where $\lambda = \dfrac{c\beta(1+mL_0)}{c\beta-\ell ms}$

then as the value of α (bifurcation parameter) passes through α_0, we get 'small amplitude' periodic solutions of (3.39), which bifurcate from the equilibrium state E^*, given by (3.40).

Proof: The condition (i) and (ii) guarantee the existence of the interior equilibrium E^*, given by (3.40). We will use the Hopf bifurcation theorem for vector fields to establish the appearance of the periodic solutions as one of the parameters α passes through a critical value α_0.

First let us show that when $\alpha = \alpha_0$, the spectrum of eigenvalues at E^* has one real (negative) and a pair of pure imaginary roots. The characteristic equation at E^* is given by (3.44a) i.e.

$$\mu^3 + a_1\mu^2 + a_2\mu + a_3 = 0 \qquad (3.60)$$

From (3.44b), $a_1 > 0$ and from (i), (ii) and (iii) we can show that $a_2 > 0$ and $a_3 > 0$. Using (3.44 b,c,d) and (iv) it can be shown that

$$a_1a_2-a_3 = \frac{s\lambda\alpha}{c\beta K}\left[(1 - \frac{s\lambda}{c\beta K})(1 - \frac{\gamma\ell m}{c\beta})\alpha s + \frac{\alpha\gamma s\lambda}{c\beta K} + (1 - \frac{s\lambda}{c\beta K})(s-\gamma)\ \frac{\gamma\ell mK}{\lambda} + \gamma^2\right] \qquad (3.61)$$

From (3.61) and condition (iv) we get

$$[a_1a_2-a_3]_{\alpha=\alpha_0} = 0$$

This proves that at E^* the characteristic equation has one real and two pure imaginary roots. Now for the values of α near α_0 we can assume that the characteristic roots are

$$\lambda_1 \pm i\lambda_2, \quad \lambda_3$$

The equation having these roots would be

$$(\mu-\lambda_3)[(\mu-\lambda_1)^2+\lambda_2^2] = 0$$

or

$$\mu^3 - (\lambda_3+2\lambda_1)\mu^2 + (\lambda_1^2+\lambda_2^2+2\lambda_1\lambda_3)\mu - (\lambda_1^2+\lambda_2^2)\lambda_3 = 0 \tag{3.62}$$

Now as in Section 3.5, we can prove that

$$\begin{aligned} \left.\frac{d\lambda_1}{d\alpha}\right|_{\alpha=\alpha_0} &= -\frac{1}{2}\left[\frac{1}{a_1^2+a_2}\frac{d}{d\alpha}(a_1a_2-a_3)\right]_{\alpha=\alpha_0} \\ &= -\frac{1}{2}\frac{s\lambda\alpha_0}{c\beta K}\left[(1-\frac{s\lambda}{c\beta K})(1-\frac{\gamma\ell m}{c\beta})s+\frac{\gamma s\lambda}{c\beta K}\right]\left[\frac{1}{a_1^2+a_2}\right]_{\alpha=\alpha_0} \\ &< 0 \end{aligned} \tag{3.63}$$

As in (3.34) we can show

$$\lambda_3 = -a_1 - 2\lambda_1$$

so that at $\alpha = \alpha_0$, $\lambda_3 = -a_1 < 0$. Also, as in (3.33b), we can show that comparing (3.60) and (3.62) we have

$$a_2 = \lambda_1^2 + \lambda_2^2 + 2\lambda_1\lambda_3$$

so that at $\alpha = \alpha_0$, $\lambda_2 = \sqrt{a_2(\alpha_0)}$. Thus at $\alpha = \alpha_0$, the characteristic roots are

$$-\left(\gamma + \frac{\alpha_0 s\lambda}{c\beta K}\right), \qquad \pm i\sqrt{(1-\frac{s\lambda}{c\beta K})(1-\frac{\gamma\ell m}{c\beta})\alpha_0 s + \frac{\alpha_0 s\lambda\gamma}{c\beta K}} \tag{3.64}$$

Now applying the Hopf bifurcation theorem and (3.63), (3.64), the theorem is proved.

The stability analysis of the periodic orbits can be done using the method mentioned in Marsden and McCracken but the computations are so

messy that we have deferred them to the appendix.

As a numerical example to illustrate the above, we take $c = \ell = m = s = L_0 = 1$, $B = 2$, $\gamma = 4$, $K = 8$. With these values, conditions (i), (ii) and (iii) are satisfied and the value of α_0 comes out to be 8. Hence if 8 is in the range of values of α, the equilibrium state $(3,2,\frac{3}{2}\alpha)$ bifurcates into periodic orbits.

3.7. The Case of No Interior Equilibrium.

Here we consider what happens when there is no interior equilibrium. Before we discuss this we need to know about the local stability behavior of other equilibrium states, i.e. E_1,E_2,E_3,E_4 and E_5 of the system (3.39).

$E_1(0,0,0)$: The variational matrix at E_1 is

$$M(E_1) = \begin{bmatrix} \gamma & 0 & 0 \\ 0 & \alpha & 0 \\ 0 & 0 & -s \end{bmatrix}$$

so that E_1 is unstable in u,x directions and stable in the y-direction.

$E_2(0,K,0)$:

$$M(E_2) = \begin{bmatrix} \gamma & 0 & 0 \\ 0 & -\alpha & -\beta K \\ 0 & 0 & -s+c\beta K \end{bmatrix}$$

The eigenvalues of $M(E_2)$ are $\gamma,-\alpha,-s+c\beta K$. Thus E_2 is unstable in the u-direction, stable in the x-direction but the stability in the y-direction depends upon the sign of the expression $(-s+c\beta K)$, so that

$$c\beta > \frac{s}{K} \Rightarrow \text{unstable in the y-direction}$$

$$c\beta \leq \frac{s}{K} \Rightarrow \text{stable in the y-direction.}$$

The latter case, in which E_2 is stable in the y-direction, shows that even if there is an abundance of prey the predator population declines. This could happen if the predators are unable to capture prey or there is some other agency which deters the predator from feeding upon the prey. It can be shown that in this case the predator population goes to extinction. From (3.39)

$$y' = y(-s + \frac{c\beta x}{1+mu}) \ .$$

We can assume that $\exists \ T_0 \ni$ for $t \geq T_0$ $x \leq K$, then

$$y' \leq y(-s+c\beta K).$$

Using the comparison equation

$$z' = z(-s+c\beta K)$$
$$z(T_0) = y(T_0) \quad ,$$

it follows that

$$y(t) \leq y(T_0)e^{(-s+c\beta K)t} \qquad t \geq T_0$$

so that $y(t) \to 0$ as $t \to \infty$. Extinction, as modelled by our system (3.39), cannot occur in a finite time. We will show later that in this particular case, the system does not permit an interior equilibrium.

$E_3(L_0,0,0)$: The variational matrix at E_3 is given by

$$M(E_3) = \begin{bmatrix} -\gamma & \gamma\ell & 0 \\ 0 & \alpha & 0 \\ 0 & 0 & -s \end{bmatrix}.$$

The eigenvalues of $M(E_3)$ are $-\gamma,\alpha,-s$. Thus E_3 attracts in the u, y directions and repels in the x-direction.

$E_4\left(0, \frac{s}{c\beta}, \frac{\alpha}{\beta}(1-\frac{s}{c\beta K})\right)$: In this case

$$M(E_4) = \begin{bmatrix} \gamma & 0 & 0 \\ \frac{ms\alpha}{c\beta}(1-\frac{s}{c\beta K}) & -\frac{\alpha s}{c\beta K} & -\frac{s}{c} \\ -\frac{ms\alpha}{\beta}(1-\frac{s}{c\beta K}) & c\alpha(1-\frac{s}{c\beta K}) & 0 \end{bmatrix}.$$

The eigenvalues of $M(E_4)$ are $\gamma,\lambda_1,\lambda_2$ where λ_1,λ_2 are given by the equations

$$\lambda_1 + \lambda_2 = -\frac{\alpha s}{c\beta K}$$

$$\lambda_1\lambda_2 = \alpha s(1-\frac{s}{c\beta K}).$$

Thus we find that E_4 is unstable in the u-direction and it is asymptotically stable in the x,y plane. We also note here that E_4 does not exist in the case $c\beta < \frac{s}{K}$.

$E_5(L_0+\ell K,K,0)$: The variational matrix at E_5 assumes the form

$$M(E_5) = \begin{bmatrix} -\gamma & \gamma\ell & 0 \\ 0 & -\alpha & \frac{-\beta K}{1+m(L_0+\ell K)} \\ 0 & 0 & -s+\frac{c\beta K}{1+m(L_0+\ell K)} \end{bmatrix}$$

The eigenvalues of $M(E_5)$ are

$$-\gamma, \quad -\alpha, \quad \left(-s + \frac{c\beta K}{1+m(L_0+\ell K)}\right)$$

so that E_5 is stable in the u,x directions but the stability in the y-direction is determined by the sign of the third eigenvalue

$$c\beta > s\left(m\ell + \frac{1+mL_0}{K}\right) \implies \text{unstable in the y-direction}$$

$$c\beta \leq s\left(m\ell + \frac{1+mL_0}{K}\right) \implies \text{stable in the y-direction.}$$

Now we consider the circumstances, in which there is no interior equilibrium. From (3.40), we find that there are two cases in which this can occur.

I. $c\beta < \ell ms$

II. $\ell ms < c\beta < \frac{s\lambda}{K}$.

Now we show that in both the above cases the equilibrium state E_5 is asymptotically stable in all the three directions. For this we need to show that

$$-s + \frac{c\beta K}{1+m(L_0+\ell K)} < 0$$

Consider the case I

$$\begin{aligned}-s + \frac{c\beta K}{1+m(L_0+\ell K)} &= \frac{-s(1+mL_0)-m\ell sK+c\beta K}{1+mL_0+m\ell K} \\ &= \frac{-s(1+mL_0)+K(c\beta-m\ell s)}{1+mL_0+m\ell K} \\ &< 0\end{aligned}$$

In the case II

$$c\beta < \frac{s\lambda}{K} = \frac{s}{K}\left\{\frac{c\beta(1+mL_0)}{c\beta-\ell ms}\right\} \Rightarrow 1 < \frac{s}{K}\left(\frac{1+mL_0}{c\beta-\ell ms}\right)$$

multiplying both the sides of this inequality by $K(c\beta-\ell ms) > 0$, we get

$$(c\beta-\ell ms)K < s(1+mL_0)$$

This again implies that

$$-s + \frac{c\beta K}{1+m(L_0+\ell K)} < 0$$

Thus we have established that if there is no interior equilibrium then E_5 is asymptotically stable (locally).

Theorem 3.11. If $c\beta < \frac{s}{K}$ then the equilibrium state $E_5(L_0+\ell K,K,0)$ is globally asymptotically stable in $\mathbb{R}^3_+$.

Proof: Let $(u(t),x(t),y(t))$ represent a solution to (3.39) with initial conditions $u(t_0) = u_0$, $x(t_0) = x_0$, $y(t_0) = y_0$, defined for all $t \geq t_0$. Then

$$c^+ = \{(u(t),x(t),y(t));\ \ t_0 \leq t < \infty\}$$

is a semiorbit of (3.39). As established earlier in E_2, we can prove that in this case

$$\lim_{t\to\infty} y(t) = 0$$

so that $L(c^+)$ lies in the u,x plane. The theorem then follows from Theorem 3.3.

Observations: In the absence of the mutualist (or $m = 0$), the predator prey system is

$$x' = \alpha x(1 - \frac{x}{K}) - \beta xy$$

$$y' = y(-s+c\beta x)$$

Using the notations given in Freedman (1980), the sign of

$$H(x^*) = x^* g_x(x^*) + g(x^*) - \frac{x^* g(x^*) p_x(x^*)}{p(x^*)}$$

decides the stability of the equilibrium position

$$\left(\frac{s}{c\beta}, \frac{\alpha}{\beta}(1 - \frac{s}{c\beta K})\right)$$

In this case $H(x^*) = -\frac{\alpha s}{c\beta K} < 0$, so that the interior equilibrium is stable. Now we want to show that when the mutualist is introduced into this system, existence of the interior equilibrium depends on the parameter m in such a way that there exists a critical value m^* of m given by

$$m^* = \frac{c\beta K - s}{sL_0 + \ell sK}$$

such that if $m > m^*$ then there is no interior equilibrium. It can be shown that $m > m^* \Rightarrow y^* = \frac{\alpha}{\beta}\lambda(1 - \frac{s\lambda}{c\beta K}) < 0$. For the values of $m < m^*$, we always have an interior equilibrium given by (3.40). We also observe that if m is small then it has a positive effect on the whole community in the sense that equilibrium population level of all the species is enhanced compared to the case when there is no mutualist.

Calculating the partial derivatives of u^*, x^*, y^* with respect to the parameter m, we find that

$$\frac{\partial u^*}{\partial m} = \frac{\ell s}{c\beta}\left(\frac{\partial\lambda}{\partial m}\right)$$

$$\frac{\partial x^*}{\partial m} = \frac{s}{c\beta}\left(\frac{\partial\lambda}{\partial m}\right)$$

$$\frac{\partial y^*}{\partial m} = \frac{\alpha}{\beta}\left(1 - \frac{2s\lambda}{c\beta K}\right)\left(\frac{\partial\lambda}{\partial m}\right)$$

where $$\frac{\partial\lambda}{\partial m} = \frac{c\beta(c\beta L_0 + \ell s)}{(c\beta - \ell m s)^2} > 0$$

These relations show that u^*, x^* populations increase with the increase of m but the change in y^* depends upon the sign of the factor $\left(1 - \frac{2s\lambda}{c\beta K}\right)$. It can be shown that if

$$m < \frac{c\beta K - 2s}{2sL_0 + \ell s K} = (m_* \text{ say}) \quad \text{then} \quad 1 - \frac{2s\lambda}{c\beta K} > 0.$$

Thus we find that as long as $m < m_*$ $(< m^*)$, the interaction with the mutualist is helpful to each species in the community. A similar result has been obtained by Thomas G. Hallan (1980), while studying the effect of cooperation on competitive systems. But if $m_* < m < m^*$ then we observe that the equilibrium population level of the species u and x goes up but that of y declines. This means that there are many mutualists protecting the prey from being attacked by predators and thereby causing non-availability of food to predators in spite of the abundance of the prey.

In the case $c\beta$ is very small, we have already shown that predation is so poor that the predators cannot survive and the interior equilibrium in the u,x plane is a global attractor in $\mathbb{R}^2_+$.

As regards the stability of the interior equilibrium (u^*,x^*,y^*), we find that it continues to be stable as in two dimensions (i.e. in the absence of the mutualist) if $s \geq \gamma$ (Corollary 3.9). Thus the relative magnitude of these parameters is important. We also find that the growth rate of the prey species (i.e. α) plays a very important role. When $\gamma > s$, then there exists a critical value α_0 of α such that if α goes below α_0, then there is a change in the stability of the equilibrium state. $\alpha = \alpha_0$ becomes the bifurcation point and we find that close to α_0, the system exhibits periodic oscillations.

3.8. Summary.

In this chapter a predator-prey-mutualist system has been modelled and mathematically analyzed. Conditions for equilibria were given, and the stability of these equilibria determined. Conditions were also given for the existence of three-dimensional periodic solutions. A specific example was discussed.

It was found that by adding a mutualist to the system, the prey equilibrium value is increased. This has the effect in the case of a stable interaction of increasing the effective carrying capacity for the prey. Further the carrying capacity for the mutualist is also increased. However, as expected, all populations remain bounded.

Depending on the parameters, adding a mutualist to the system could be either stabilizing or destabilizing, and therefore limit cycles could appear, where they were not before, or disappear.

Finally, adding a mutualist to a predator-prey system could cause the predator to go extinct, in which case the prey and mutualist population numbers approach equilibrium values.

CHAPTER IV

COMPETITOR - COMPETITOR - MUTUALIST MODEL

Study of models of competition was started as early as 1920's by Lotka (1925) and Volterra (1931). The models considered were just the extension of the single species logistic equation:

$$x_1' = \gamma_1 x_1 [1 - \frac{1}{K_1} (x_1 + \alpha_{12} x_2)]$$

$$x_2' = \gamma_2 x_2 [1 - \frac{1}{K_2} (x_2 + \alpha_{21} x_1)]$$

where $\gamma_1, K_1, \alpha_{12}$ are the intrinisic growth rate, carrying capacity and the competition coefficient (which measures the inhibitory effect of x_2 upon x_1), respectively, of the species x_1, and $\gamma_2, K_2, \alpha_{21}$ are similar parameters for the species x_2. The stability properties of this model are well known. In particular, when the two species use the resources in the identical fashion (whence $\alpha_{12} = \alpha_{21} = 1$ and $K_1 = K_2$); it is known that both species cannot persist. This led to the 'competitive exclusion principle', that species which make their livings in identical ways cannot stably coexist in a stable environment (May, 1976) is confirmed in the study of simple laboratory systems. Gause (1934) and others, e.g. Levins (1974), May (1973, 1976), Pielou (1977), Roughgarden (1975) have discussed this problem.

Several more realistic models of two competing species have been analyzed by Hutchinson (1947), Cunningham (1955), Utz and Waltman (1963), Rescigno and Richardson (1967).

These models can be improved by introducing a third species in the system, which for example might help the weaker species to coexist with the other species. Hallam (1980) has discussed the effects of cooperation on competitive systems, modelled on the basis of Lotka-Volterra kinetics. He considers a system composed of a competitive subcommunity and two cooperative subcommunities and concludes that mutualism can be beneficial for all species in the community. He also shows that a mutualistic species can drive a stable competitive system to extinction.

In this chapter we shall analyze a model incorporating two competing species, x_1, x_2 and a third species u, which acts as a mutualist to the species x_1. We shall assume that there is no direct interaction between u and x_2.

4.1. General Model.

We shall suppose that the dynamics of population-growth of a competitor-competitor-mutualist community is represented by the following system of equations:

$$\left.\begin{aligned} u' &= uh(u,x_1) \\ x_1' &= \alpha x_1[g_1(x_1,u)-q_1(x_1,x_2,u)] \\ x_2' &= x_2[g_2(x_2)-q_2(x_1,x_2)] \end{aligned}\right\} \tag{4.1}$$

where u, x_1 form a mutualistic pair. The hypotheses implicit in equations (4.1) are that the rate of increase or decrease of the

populations does not depend on time and that the populations are so large as to be measurable with real numbers and not subject to random fluctuations.

We shall assume that

$$u, x_1, x_2 \in R_+$$

$$\text{and} \quad h, g_1, g_2, q_2 : R_+^2 \to R; \quad q_1 : R_+^3 \to R,$$

are continuous and sufficiently smooth functions to guarantee existence and the uniqueness of solutions to initial value problems for (4.1) with initial conditions in R_+^3, and also to allow the stability analysis of any solution of (4.1). We require the solutions to be defined on some interval $[0,T)$ where $0 < T < \infty$.

We further make the following assumptions:

(i) $h(u,x)$ satisfies conditions A(i)-A(iv) mentioned in Chapter III.

(ii) $g_1(x,u)$ satisfies conditions A(v)-A(viii) mentioned in Chapter III.

(iii) The species x_2 can grow at low densities i.e.

$$g_2(0) > 0.$$

(iv) The environment has a carrying capacity for the species x_2, i.e.

$$\exists K_2 > 0 \ni g_2(K_2) = 0.$$

(v) Multiplication of the species x_2 is slowed down by an increase in their own number. Mathematically

$$g_{2x_2}(x_2) < 0$$

i.e. the species x_2 has density dependent growth.

(vi) In the absence of the species x_2 there is no competition to species x_1, so that its growth is not inhibited. Mathematically

$$q_1(x_1,0,u) = 0 \quad \text{for all} \quad x_1,u \geq 0.$$

(vii) For a fixed population of x_1, an increase in the population of the species x_2 inhibits the growth rate of x_1, i.e.

$$q_{1x_2}(x_1,x_2,u) > 0$$

This is the competitive effect of x_2 on x_1.

(viii) For a fixed population of the species x_1 and x_2, an increase in the population of the mutualist species u, reduces the competitive effect of x_2 on x_1. Thus mathematically

$$q_{1u}(x_1,x_2,u) < 0$$

This is the main mutualistic effect of u on x_1.

(ix) Other variables remaining fixed, an increase in x_1, results in more competition, i.e.

$$q_{1x_1} \geq 0$$

(x) In the absence of the species x_1 there is no competition to species x_2, i.e.

$$q_2(0,x_2) = 0 \quad \text{for} \quad x_2 \geq 0.$$

(xi) For a fixed population of the species x_2, an increase in the population of the species x_1 slows down the growth rate of x_2, i.e.

$$q_{2x_1}(x_1,x_2) > 0.$$

This is the main effect of competition of x_1 on x_2.

(xii) $$q_{2x_2} \geq 0.$$

(xiii) The functions $q_1(x_1,x_2,u)$ and $q_2(x_1,x_2)$ are non-negative.

4.2. Boundedness of Solutions.

In this section we shall show that conditions assumed in the Section 1 ensure the boundedness of solutions of the system (4.1).

Let $u(t_0) = u_0$, $x_1(t_0) = x_{10}$ and $x_2(t_0) = x_{20} > 0$ and represent the initial population of the species at any time t_0. Then we first prove that

$$x_1(t) \leq \max\{x_{10},K_1(0)\}$$

<u>Case (i)</u>: Let $x_{10} > K_1(0)$. Then we claim that $x_1(t) \leq x_{10}$ for $t \geq t_0$. If this is not true then $\exists t_1 \geq t_0$ such that $x_1(t_1) = x_{10}$ and $x_1'(t_1) \geq 0$. But from (4.1)

$$\begin{aligned} x_1'(t_1) &= \alpha x_1(t_1)[g_1(x_1(t_1),u(t_1))-q_1(x_1(t_1),x_2(t_1),u(t_1))] \\ &= \alpha x_{10}[g_1(x_{10},u(t_1))-q_1(x_{10},x_2(t_1),u(t_1))] \\ &\le \alpha x_{10}[g_1(x_{10},0)-q_1(x_{10},x_2(t_1),u(t_1))] \\ &< 0 \quad \text{from (xiii) and the fact that } g_1(x_{10},0) < 0 \end{aligned}$$

contradiction.

Hence $x_1(t) \le x_{10}$.

Case (ii): Let $x_{10} \le K_1(0)$.

Then we claim that $x_1(t) \le K_1(0)$ for all $t \ge t_0$. If not, then $\exists t_2 \ge 0$ such that $x_1(t_2) = K_1(0)$ and $x_1'(t_2) \ge 0$.

We consider two subcases.

Subcase (i): $x_1'(t_2) > 0$.

From (4.1)

$$\begin{aligned} x_1'(t_2) &= \alpha K_1(0)[g_1(K_1(0),u(t_2))-q_1(K_1(0),x_2(t_2),u(t_2))] \\ &\le \alpha K_1(0)g_1(K_1(0),0) \quad \text{(by (ii) and (xiii))} \\ &= 0, \quad \text{contradiction.} \end{aligned}$$

Subcase (ii): $x_1'(t_2) = 0$

In this case if $g_1(K_1(0),u(t_2)) < g_1(K_1(0),0)$ then again we can get contradiction. If $g_1(K_1(0),u(t_2)) = g_1(K_1(0),0)$ and $q_1(K_1(0),x_2(t_2),u(t_2)) > 0$, then

$$x_1'(t_2) = -\alpha K_1(0)q_1(K_1(0),x_2(t_2),u(t_2)) < 0, \quad \text{contradiction.}$$

So the only case left is when

$$g_1(K_1(0),u(t_2)) = g_1(K_1(0),0) \quad \text{and} \quad q_1(K_1(0),x_2(t_2),u(t_2)) = 0.$$

In this case uniqueness of solutions to initial value problems imply that $x_1 \equiv K_1(0)$ is a solution.

Thus we have proved that $x_1(t) \leq K_1(0)$. Combining results of the above two cases we establish that

$$x_1(t) \leq \max\{x_{10},K_1(0)\} = M \quad \text{(say)}.$$

In a similar way, we can show that

$$x_2(t) \leq \max\{x_{20},K_2\} = N \quad \text{(say)}$$

Finally we prove that

$$u(t) \leq \max\{u_0,L(M)\}$$

Let $u_0 > L(M)$. Then we claim that $u(t) \leq u_0$ for all $t \geq t_0$. Suppose this is not true then

$$\exists t_3 > 0 \ni u(t_3) = u_0 \quad \text{and} \quad u'(t_3) \geq 0.$$

From (4.1)

$$\begin{aligned} u'(t_3) &= u(t_3)h\big(u(t_3),x_1(t_3)\big) \\ &= u_0h\big(u_0,x_1(t_3)\big) \\ &\leq u_0h(u_0,M) \\ &< 0 \quad \text{because} \quad h(u_0,M) < h\big(L(M),M\big) = 0 \\ &\quad \text{contradiction.} \end{aligned}$$

Hence $u(t) \leq u_0$.

Similarly we can show that if $u_0 \le L(M)$ then

$$u(t) \le L(M) \quad \text{for all} \quad t \ge t_0$$

We also observe that no trajectory of (4.1) leaves the octant R_+^3 since existence and uniqueness of solutions is assumed to hold because if $u = 0$ then $u' = 0$

$x_1 = 0$ then $x_1' = 0$

and $x_2 = 0$ then $x_2' = 0$.

Results mentioned above can be put in the following form.

Theorem 4.1. If the assumptions (i)-(v) and (Xiii) are satisfied then

$$R = \{(u,x_1,x_2): 0 \le u \le L(M);\ 0 \le x_1 \le M,\ 0 \le x_2 \le N\}$$

is a region of stability for (4.1).

Proof: We have established that any trajectory of (4.1) starting in R stays in R, hence the result.

4.3. Equilibrium States.

In this section we list all the equilibrium states of the system (4.1).

E_1: (0,0,0) is always an equilibrium state.

The conditions (ii), (iv) and (i) give the following equilibrium states

E_2: $(0, K_1(0), 0)$,

E_3: $(0, 0, K_2)$,

E_4: $(L(0), 0, 0)$.

Depending upon the number of intersections of the curves

$$u = L(x_1) \quad \text{and}$$

$$x_1 = K_1(u)$$

we shall have various equilibrium states in the u-x_1 plane. However, we can make some further assumptions on the functions $h(u, x_1)$ and $g_1(x_1, u)$, so as to guarantee the existence of a unique equilibrium state, interior to the u-x_1 plane, i.e.

E_5: $(\breve{u}, \breve{x}_1, 0)$, where $\breve{u}$, $\breve{x}_1$ are such that

$$L\big(K_1(\breve{u})\big) = \breve{u}$$

$$\text{and} \quad K_1\big(L(\breve{x}_1)\big) = \breve{x}_1 .$$

From (i) and (iv), we get the equilibrium state

E_6: $\big(L(0), 0, K_2\big)$.

Again depending upon the number of intersections of the curves

$$g_1(x_1, 0) = q_1(x_1, x_2, 0)$$

$$\text{and} \quad g_2(x_2) = q_2(x_1, x_2)$$

one can have several equilibirum states. Let us assume that $\hat{x}_1, \hat{x}_2$ solve the above equations, then the corresponding equilibrium state is

E_7: $(0,\hat{x}_1,\hat{x}_2)$

Finally, the equilibrium state of greatest interest is the one which lies interior to the first octant $(u > 0,\ x_1 > 0,\ x_2 > 0)$. Any equilibrium state of this kind will be obtained by solving the following system of algebraic equations:

$$h(u,x_1) = 0$$

$$g_1(x_1,u) = q_1(x_1,x_2,u)$$

$$g_2(x_2) = q_2(x_1,x_2)$$

From (i) we get $u = L(x_1)$, so that the existence of such equilibrium depends upon the solution of simultaneous equations

$$g_1\big(x_1,L(x_1)\big) = q_1\big(x_1,x_2,L(x_1)\big)$$

$$g_2(x_2) = q_2(x_1,x_2)$$

Let us assume that $\bar{x}_1$, $\bar{x}_2$ solve these equations, then we have the required interior equilibrium state

E_8: $(\bar{u},\bar{x}_1,\bar{x}_2)$ where $\bar{u} = L(\bar{x}_1)$.

4.4. Stability of Equilibria.

The variational matrix for the system (4.1) is given by

$$M(u,x_1,x_2) = \begin{bmatrix} h(u,x_1)+uh_u(u,x_1) & uh_{x_1}(u,x_1) & 0 \\ \alpha x_1\{g_{1u}(x_1,u)-q_{1u}(x_1,x_2,u)\} & \begin{matrix}[\alpha\{g_1(x_1,u)-q_1(x_1,x_2,u)\} \\ +\alpha x_1\{g_{1x_1}(x_1,u) \\ -q_{1x_1}(x_1,x_2,u)\}]\end{matrix} & -\alpha x_1 q_{1x_2}(x_1,x_2,u) \\ 0 & -x_2 q_{2x_1}(x_1,x_2) & \begin{matrix} g_2(x_2)-q_2(x_1,x_2) \\ +x_2\{g_{2x_2}(x_2) \\ -q_{2x_2}(x_1,x_2)\}\end{matrix} \end{bmatrix}$$

Now we consider various equilibrium states separately.

$E_1(0,0,0)$: From (4.2), we can compute the characteristic equation for E_1. As mentioned in Chapter II, it is given by

$$\begin{vmatrix} h(0,0)-\lambda & 0 & 0 \\ 0 & \alpha g_1(0,0)-\lambda & 0 \\ 0 & 0 & g_2(0)-\lambda \end{vmatrix} = 0$$

Since $h(0,0)$, $g_1(0,0)$, $g_2(0) > 0$, this equilibrium state is unstable in all directions. So that all populations grow near E_1. This also shows that all the populations cannot go to zero, simultaneously.

$E_2(0,K_1(0),0)$: The characteristic equation for E_2 is

$$\begin{vmatrix} h(0,K_1(0))-\lambda & 0 & 0 \\ \alpha K_1(0)\{g_{1u}(K_1(0),0) & \alpha K_1(0)\{g_{1x_1}(K_1(0),0) & -\alpha K_1(0)q_{1x_2}(K_1(0),0,0) \\ -q_{1u}(K_1(0),0,0)\} & -q_{1x_1}(K_1(0),0,0)\}-\lambda & \\ 0 & 0 & g_2(0)-q_2(K_1(0),0)-\lambda \end{vmatrix} = 0$$

The eigenvalues are $h(0,K_1(0))$, $\alpha K_1(0)\{g_{1x_1}(K_1(0),0)-q_{1x_1}(K_1(0),0,0)\}$ and $\{g_2(0)-q_2(K_1(0),0)\}$. From (i), (ii) and (ix) we find that E_2 is unstable in the u-direction, stable in the x_1-direction and the stability in the x_2-direction depends upon the sign of the expression $\{g_2(0)-q_2(K_1(0),0)\}$. However E_2 is unstable.

$E_3(0,0,K_2)$: The characteristic equation for E_3 is

$$\begin{vmatrix} h(0,0)-\lambda & 0 & 0 \\ 0 & \alpha\{g_1(0,0)-q_1(0,K_2,0)\}-\lambda & 0 \\ 0 & -K_2q_{2x_1}(0,K_2) & K_2\{g_{2x_2}(K_2)-q_{2x_2}(0,K_2)\}-\lambda \end{vmatrix} = 0$$

The eigenvalues are $h(0,0)$, $\alpha\{g_1(0,0)-q_1(0,K_2,0)\}$ and $K_2\{g_{2x_2}(K_2)-q_{2x_2}(0,K_2)\}$. Thus near E_3, u-population grows, x_2-population declines and the behaviour of x_1 depends upon the sign of the expression $\{g_1(0,0)-q_1(0,K_2,0)\}$. Certainly E_3 is unstable.

$E_4(L(0),0,0)$: The characteristic equation at E_4 is given by

$$\begin{vmatrix} L(0)h_u\big(L(0),0\big)-\lambda & L(0)h_{x_1}\big(L(0),0\big) & 0 \\ 0 & \alpha g_1\big(0,L(0)\big)-\lambda & 0 \\ 0 & 0 & g_2(0)-\lambda \end{vmatrix} = 0$$

This shows that E_4 is stable in u-direction but unstable in x_1, x_2 directions. At low population levels of x_1 and x_2, the effect of the mutualist is negligible.

Next we consider the equilibria lying in the planes.

$E_5(\tilde{u},\tilde{x}_1,0)$: The characteristic equation at E_5 is given by

$$\begin{vmatrix} uh_u(\tilde{u},\tilde{x}_1)-\lambda & \tilde{u}h_{x_1}(\tilde{u},\tilde{x}_1) & 0 \\ \alpha\tilde{x}_1\{g_{1u}(\tilde{x}_1,\tilde{u})-q_{1u}(\tilde{x}_1,0,\tilde{u})\} & \begin{matrix}\alpha\tilde{x}_1\{g_{1x_1}(\tilde{x}_1,\tilde{u}) \\ -q_{1x_1}(\tilde{x}_1,0,\tilde{u})\}-\lambda\end{matrix} & -\alpha\tilde{x}_1 q_{1x_2}(\tilde{x}_1,0,\tilde{u}) \\ 0 & 0 & \{g_2(0)-q_2(\tilde{x}_1,0)\}-\lambda \end{vmatrix} = 0$$

The eigenvalues are given by the roots of the equation

$$\begin{aligned}[g_2(0)-q_2(\tilde{x}_1,0)-\lambda][\lambda^2-\lambda\{\tilde{u}h_u(\tilde{u},\tilde{x}_1)+\alpha\tilde{x}_1\big(g_{1x_1}(\tilde{x}_1,\tilde{u})-q_{1x_1}(\tilde{x}_1,0,\tilde{u})\big)\} \\ +\alpha\tilde{u}\tilde{x}_1\{h_u(\tilde{u},\tilde{x}_1)\big(g_{1x_1}(\tilde{x}_1,\tilde{u})-q_{1x_1}(\tilde{x}_1,0,\tilde{u})\big) \\ -h_{x_1}(\tilde{u},\tilde{x}_1)\big(g_{1u}(\tilde{x}_1,\tilde{u})-q_{1u}(\tilde{x}_1,0,\tilde{u})\big)\}] = 0\end{aligned}$$

If the roots are denoted by $\lambda_1,\lambda_2,\lambda_3$ then

$$\lambda_3 = g_2(0) - q_2(\breve{x}_1,0),$$

$$\lambda_1 + \lambda_2 = \breve{u}h_u(\breve{u},\breve{x}_1) + \alpha\breve{x}_1\{g_{1x_1}(\breve{x}_1,\breve{u})-q_{1x_1}(\breve{x}_1,o,\breve{u})\} < 0$$

$$\lambda_1\lambda_2 = \alpha\breve{u}\breve{x}_1[h_u(\breve{u},\breve{x}_1)\{g_{1x_1}(\breve{x}_1,\breve{u})-q_{1x_1}(\breve{x}_1,0,\breve{u})\}$$
$$-hx_1(\breve{u},\breve{x}_1)\{g_{1u}(\breve{x}_1,\breve{u})-q_{1u}(\breve{x}_1,0,\breve{u})\}]$$

If we assume $g_{1u} \leq 0$ then $\lambda_1 \cdot \lambda_2 > 0$, so that in this case E_5 is asymptotically stable in the u, x_1 plane. The stability in the x_2-direction depends upon the sign of $\{g_2(0)-q_2(\breve{x}_1,0)\}$. In case we assume that $g_{1u} > 0$, then after Rescigno and Richardson by making further assumptions

$$uh_u(u,x_1) + x_1h_{x_1}(x_1,u) \leq -\alpha_1 < 0$$
$$ug_{1u}(x_1,u) + x_1g_{1x_1}(x_1,u) \leq -\alpha_1 < 0$$

We can still have the same conclusion as above.

$E_6\big(L(0),0,K_2\big)$: The variational matrix at E_6, assumes the form

$$M(E_6) = \begin{bmatrix} L(0)h_u\big(L(0),0\big) & L(0)h_{x_1}\big(L(0),0\big) & 0 \\ 0 & \alpha\{g_1\big(0,L(0)\big)-q_1\big(0,K_2,L(0)\big)\} & 0 \\ 0 & -K_2q_{2x_1}(0,K_2) & K_2\{g_{2x_2}(K_2)-q_{2x_2}(0,K_2)\} \end{bmatrix}$$

The eigenvalues of this matrix are

$L(0)h_u(L(0),0)$, $\alpha\{g_1(0,L(0))-q_1(0,K_2,L(0))\}$ and $K_2\{g_{2x_2}(K_2)-q_{2x_2}(0,K_2)\}$

This shows that near E_6, u, x_2 populations are stable whereas the stability in the x_1-direction depends upon the sign of the expression $\alpha\{g_1(0,L(0))-q_1(0,K_2,L(0))\}$.

$E_7(0,\hat{x}_1,\hat{x}_2)$: As mentioned earlier there may be several equilibria in the x_1, x_2 plane. The characteristic equation, in this case, is given by

$$\begin{vmatrix} h(0,\hat{x}_1)-\lambda & 0 & 0 \\ \begin{array}{l}\alpha\hat{x}_1\{g_{1u}(\hat{x}_1,0)\\ -q_{1u}(\hat{x}_1,\hat{x}_2,0)\}\end{array} & \begin{array}{l}\alpha\hat{x}_1\{g_{1x_1}(\hat{x}_1,0)\\ -q_{1x_1}(\hat{x}_1,\hat{x}_2,0)\}-\lambda\end{array} & -\alpha\hat{x}_1 q_{1x_2}(\hat{x}_1,\hat{x}_2,0) \\ 0 & -\hat{x}_2 q_{2x_1}(\hat{x}_1,\hat{x}_2) & \hat{x}_2\{g_{2x_2}(\hat{x}_2)-q_{2x_2}(\hat{x}_1,\hat{x}_2)\}-\lambda \end{vmatrix} = 0$$

The eigenvalues $\lambda_1,\lambda_2,\lambda_3$ (say) will be given by

$$\lambda_1 = h(0,x_1) > 0$$

$$\lambda_2 + \lambda_3 = \alpha\hat{x}_1\{g_{1x_1}(\hat{x}_1,0)-q_{1x_1}(\hat{x}_1,\hat{x}_2,0)\} + \hat{x}_2\ g_{2x_2}(\hat{x}_2)-q_{2x_2}(\hat{x}_1,\hat{x}_2)\}$$

$$\lambda_2\lambda_3 = \alpha\hat{x}_1\hat{x}_2[\{g_{1x_1}(\hat{x}_1,0)-q_{1x_1}(\hat{x}_1,\hat{x}_2,0)\}\{g_{2x_2}(\hat{x}_2)-q_{2x_2}(\hat{x}_1,\hat{x}_2)\} -q_{1x_2}(\hat{x}_1,\hat{x}_2,0)q_{2x_1}(\hat{x}_1,\hat{x}_2)]$$

According to Rescigno and Richardson (1967), the positive quadrant of the plane (x_1,x_2) can be divided into three zones:

Zone I, where $g_1(x_1,0) - q_1(x_1,x_2,0) > 0$; $g_2(x_2) - q_2(x_1,x_2) > 0$;

Zone II, where $g_1(x_1,0) - q_1(x_1,x_2,0) < 0$; $g_2(x_2) - q_2(x_1,x_2) < 0$

and Zone III, where $\{g_1(x_1,0)-q_1(x_1,x_2,0)\}\{g_2(x_2)-q_2(x_1,x_2)\} \leq 0$.

Zone III, formed by the curves $g_1(x_1,0) = q_1(x_1,x_2,0)$, $g_2(x_2) = q_2(x_1,x_2)$, contains the points enclosed by them in $\mathbb{R}_+^2$. The stability of the equilibrium depends upon the sign of λ_2,λ_3, which is given above. If $\lambda_2\lambda_3 > 0$ then E_7 is stable in (x_1,x_2) because $\lambda_2 + \lambda_3 < 0$ but if $\lambda_2\lambda_3 < 0$ then E_7 is a hyperbolic point in the plane. In all these cases the u-population grows near the (x_1,x_2) plane.

$E_8(\bar{u},\bar{x}_1,\bar{x}_2)$: Finally we consider the interior equilibrium. The variational matrix at E_8 is given by

$$M(\bar{u},\bar{x}_1,\bar{x}_2) = \begin{bmatrix} \bar{u}h_u(\bar{u},\bar{x}_1) & \bar{u}h_{x_1}(\bar{u},\bar{x}_1) & 0 \\ \alpha\bar{x}_1\{g_{1u}(\bar{x}_1,\bar{u}) & \alpha x_1\{(g_{1x_1}(\bar{x}_1,\bar{u}) & -\alpha x_1 q_{1x_2}(\bar{x}_1,\bar{x}_2,\bar{u}) \\ -q_{1u}(\bar{x}_1,\bar{x}_2,\bar{u})\} & -q_{1x_1}(\bar{x}_1,\bar{x}_2,\bar{u}))\} & \\ 0 & -x_2 q_{2x_1}(\bar{x}_1,\bar{x}_2) & +\bar{x}_2\{g_{2x_2}(\bar{x}_2) \\ & & -q_{2x_2}(\bar{x}_1,\bar{x}_2)\} \end{bmatrix} \quad (4.3)$$

The eigenvalues $\lambda_1,\lambda_2,\lambda_3$ (say) of this matrix satisfy the following relations:

$$\lambda_1+\lambda_2+\lambda_3 = -a_1 \equiv \bar{u}h_u(\bar{u},\bar{x}_1) + \alpha\bar{x}_1\{g_{1x_1}(\bar{x}_1,\bar{u})-q_{1x_1}(\bar{x}_1,\bar{x}_2,\bar{u})\}$$
$$+ \bar{x}_2\{g_{2x_2}(\bar{x}_2)-q_{2x_2}(\bar{x}_1,\bar{x}_2)\}$$

$$\lambda_1\lambda_2+\lambda_2\lambda_3+\lambda_3\lambda_1 = a_2 \equiv \bar{u}h_u(\bar{u},\bar{x}_1)[\alpha\bar{x}_1\{g_{1x_1}(\bar{x}_1,\bar{u})-q_{1x_1}(\bar{x}_1,\bar{x}_2,\bar{u})\}$$
$$+ \bar{x}_2\{g_{2x_2}(\bar{x}_2)-q_{2x_2}(\bar{x}_1,\bar{x}_2)\}] + \alpha\bar{x}_1\bar{x}_2[\{g_{1x_1}(\bar{x}_1,\bar{u})$$
$$-q_{1x_1}(\bar{x}_1,\bar{x}_2,\bar{u})\}\{g_{2x_2}(\bar{x}_2)-q_{2x_2}(\bar{x}_1,\bar{x}_2)\}$$
$$- q_{1x_2}(\bar{x}_1,\bar{x}_2\bar{u})q_{2x_1}(\bar{x}_1,\bar{x}_2)] - \alpha\bar{u}\bar{x}_1h_{x_1}(\bar{u},\bar{x}_1)\{g_{1u}(\bar{x}_1,\bar{u})$$
$$-q_{1u}(\bar{x}_1,\bar{x}_2,\bar{u})\}$$

and

$$\lambda_1\lambda_2\lambda_3 = -a_3 \equiv \alpha\bar{u}\bar{x}_1\bar{x}_2[h_u(\bar{u},\bar{x}_1)\{\big(g_{1x_1}(\bar{x}_1,\bar{u})-q_{1x_1}(\bar{x}_1,\bar{x}_2,\bar{u})\big)\big(g_{2x_2}(\bar{x}_2)$$
$$-q_{2x_2}(\bar{x}_1,\bar{x}_2)\big)-q_{1x_2}(\bar{x}_1,\bar{x}_2,\bar{u})q_{2x_1}(\bar{x}_1,\bar{x}_2)\} - h_{x_1}(\bar{u},\bar{x}_1)\{g_{1u}(\bar{x}_1,\bar{u})$$
$$-q_{1u}(\bar{x}_1,\bar{x}_2,\bar{u})\}\{g_{2x_2}(\bar{x}_2)-q_{2x_2}(\bar{x}_1,\bar{x}_2)\}] \tag{4.4}$$

We now make a change of variables in the system (4.1) as follows

$$\begin{aligned} u - \bar{u} &= \xi \\ x_1 - \bar{x}_1 &= \eta \\ x_2 - \bar{x}_2 &= \zeta \end{aligned} \tag{4.5}$$

and introduce

$$x = (\xi,\eta,\zeta)^T \quad \text{(column vector)} \tag{4.6}$$

Then the system (4.1) can be represented in the form

$$x' = Ax + F(x) \tag{4.7}$$

where the matrix

$$A = M(\bar{u},\bar{x}_1,\bar{x}_2) \tag{4.8}$$

and $F(x)$ is a column vector given by

$$F(x) = \begin{bmatrix} F_1(\xi,\eta,\zeta;\ \bar{u},\bar{x}_1,\bar{x}_2) \\ F_2(\xi,\eta,\zeta;\ \bar{u},\bar{x}_1,\bar{x}_2) \\ F_3(\xi,\eta,\zeta;\ \bar{u},\bar{x}_1,\bar{x}_2) \end{bmatrix} \tag{4.9}$$

where

$$F_1(\xi,\eta,\zeta;\ \bar{u},\bar{x}_1,\bar{x}_2) = (\xi+\bar{u})h(\xi+\bar{u},\eta+\bar{x}_1) - \bar{u}h_u(\bar{u},\bar{x}_1)\xi - \bar{u}h_{x_1}(\bar{u},\bar{x}_1)\eta$$

$$\begin{aligned} F_2(\xi,\eta,\zeta;\ \bar{u},\bar{x}_1,\bar{x}_2) = {} & \alpha(\eta+\bar{x}_1)[g_1(\eta+\bar{x}_1,\xi+\bar{u})-q_1(\eta+\bar{x}_1,\zeta+\bar{x}_2,\xi+\bar{u})] \\ & -\alpha\bar{x}_1\{g_{1u}(\bar{x}_1,\bar{u})-q_{1u}(\bar{x}_1,\bar{x}_2,\bar{u})\}\xi + \alpha\bar{x}_1 q_{1x_2}(\bar{x}_1,\bar{x}_2,\bar{u})\zeta \\ & -\alpha\bar{x}_1\{g_{1x_1}(\bar{x}_1,\bar{u})-q_{1x_1}(\bar{x}_1,\bar{x}_2,\bar{u})\}\eta \end{aligned}$$

and

$$\begin{aligned} F_3(\xi,\eta,\zeta;\ \bar{u},\bar{x}_1,\bar{x}_2) = {} & (\zeta+\bar{x}_2)[g_2(\zeta+\bar{x}_2)-q_2(\eta+\bar{x}_1,\zeta+\bar{x}_2)] + \bar{x}_2 q_{2x_1}(\bar{x}_1,\bar{x}_2)\eta \\ & + \bar{x}_2\{g_{2x_2}(\bar{x}_2)-q_{2x_2}(\bar{x}_1,\bar{x}_2)\}\zeta \end{aligned} \tag{4.10}$$

The linear approximation of system (4.1) near the equilibrium state $(\bar{u},\bar{x}_1,\bar{x}_2)$ is given by

$$x' = Ax \tag{4.11}$$

Theorem 4.2. Let us assme that the system (4.1) has a unique

interior equilibrium $(\bar{u},\bar{x}_1,\bar{x}_2) \in \mathbb{R}^3_+$. Also let

(i) $a_1 > 0$, $a_3 > 0$ and $a_1 a_2 > a_3$.

(ii) $\lim_{\|x\|\to 0} \left\{\frac{\|F(x)\|}{\|x\|}\right\} = 0$.

Then $x(t) = 0$, $t \geq t_0$ for any t_0 is an asymptotically stable solution of (4.7), where a_1,a_2,a_3 are given by (4.4).

Proof: This is proved exactly the same way as the theorem (3.5).

4.5. Persistence in Model (4.1).

We first define (after Gard and Hallam, 1979) extinction and persistence with reference to our model (4.1). The system (4.1) will be said to have a solution which goes to extinction provided there is a trajectory c^+ of (4.1) where

$$c^+ = \{(u(t),x_1(t),x_2(t)) : (u(t_0),x_1(t_0),x_2(t_0)) \in \mathbb{R}^3_+ ;\ t \geq t_0\} \tag{4.12}$$

such that at least one of $u(t)$, $x_1(t)$, or $x_2(t)$ approaches zero as t approaches infinity. When no solution of (4.1) goes to extinction, the system is said to be persistent.

Theorem 4.3. Let the following conditions hold, in addition to those mentioned in Section 1.

(i) $\min\{(g_1(0,0)-q_1(0,K_2,0)),\ (g_1(0,L(0))-q_1(0,K_2,L(0)))\} > 0$

(ii) $\min\{(g_2(0)-q_2(K_1(0),0)),\ (g_2(0)-q_2(\tilde{x}_1,0))\} > 0$

(iii) $g_{1u}(x_1,u) > 0$

(iv) $uh_u(u,x_1)+x_1h_{x_1}(x_1,u) \le -\alpha_1 < 0$; $ug_{1u}(x_1,u)+x_1g_{1x_1}(x_1,u) \le -\alpha_1 < 0$

Then the system (4.1) is persistent.

Proof: First we show that the component $u(t)$ can never go to zero. Let $\delta > 0$ be given such that $\delta < L(0)$. Then if $t \ge t_0$ is such that $u(t) \le \delta$, then

$$u'(t) = u(t)h\big(u(t),x_1(t)\big) \ge u(t)h\big(\delta,x_1(t)\big) > 0$$

and hence there cannot exist any sequence $t_n \to \infty \ni u(t_n) \to 0$.

The other cases in which a solution to (4.1) can go to extinction are when $x_1(t) \to 0$ as $t \to \infty$

or $x_2(t) \to 0$ as $t \to \infty$

or both $x_1(t)$, $x_2(t)$ go to zero, simultaneously at $t \to \infty$.

We claim that the components $x_1(t)$, $x_2(t)$ of c^+, cannot go to zero simultaneously. Because if they do then for sufficiently large t, $u(t)$ is close to $L(0)$ and the per capita growth rate of x_1 is

$$\alpha[g_1\big(0,L(0)\big)] > 0 \quad \text{from (i)}$$

and consequently $x_1(t) \not\to 0$ as $t \to \infty$, contradiction.

Next suppose that the component $x_1(t) \to 0$ as $t \to \infty$ while $x_2(t)$ and $u(t)$ persist. If this happens then for sufficiently large t, $u(t)$ is close to its carrying capacity $L(0)$, x_2 is close to its carrying capacity K_2 and the per capita growth rate of

x_1 is given by

$$[g_1(0,L(0))-q_1(0,K_2,L(0))] > 0 \quad \text{from (i).}$$

But this implies that $x_1(t) \not\to 0$ as $t \to \infty$, contradiction!

Finally, suppose that the species x_2 goes to extinction while u and x_1 persist. Then, again for sufficiently large t, $x_1(t) \to \breve{x}_1$ as $t \to \infty$ because it has been shown by Albrecht et al. (1974) that under the additional conditions (iii) and (iv) E_5 is globally asymptotically stable in $\mathbb{R}_+^2$. So that the per capita growth rate of x_2 for sufficiently large t is given by the expression

$$[g_2(0)-q_2(\breve{x}_1,0)] > 0 \quad \text{from (ii)}$$

But this implies that $x_2(t) \not\to 0$ as $t \to \infty$, which gives contradiction.

Conditions (i) and (ii) also guarantee that when the u-population is at very low level, neither x_1 nor x_2 goes to extinction.

Thus we have exhausted all possible cases of extinction. This proves the theorem.

Note: Expressions involved in the conditions (i) and (ii) are for different eigenvalues of the variational matrix near the equilibrium states. For example $\{g_1(0,L(0))-q_1(0,K_2,L(0))\}$ is one of the eigenvalues of the variational matrix at (E_6), as shown earlier in Section 4. If this expression is negative then it can be shown that the real parts of all the eigenvalues at (E_6) are negative. In that

case, by considering the linear approximation of the system (4.1) near (E_6), we can find a strong Liapunov function for the linearized system and thereby establish the existence of a region wherein each solution of the non-linear system that is initially in the region has component x_1 which goes to extinction.

Similarly if $\{g_2(0)-q_2(\tilde{x}_1,0)\} < 0$, then there exists a region in $\mathbb{R}_+^3$ bounded by (u,x_1) plane, wherein each solution that is initially in the region has component x_2 which goes to extinction.

4.6. A Special Case.

In this section we consider a special case of the model (4.1), which has most of its features. Let the dynamics of species growth be given by

$$
\begin{aligned}
u' &= \gamma u\left(1 - \frac{u}{L_0+\ell x_1}\right) \\
x_1' &= \alpha x_1\left(1 - \frac{x_1}{K_1}\right) - \frac{\alpha\beta x_1 x_2}{1+mu} \\
x_2' &= \delta x_2\left(1 - \frac{x_2}{K_2}\right) - \eta x_1 x_2,
\end{aligned}
\tag{4.12}
$$

where K_1, K_2 are carrying capacities of the species x_1 and x_2 respectively. Parameters $m,\ell,L_0,\alpha,\beta,\gamma,\delta,\eta$ are all assumed to be positive. In the absence of the mutualist (u), the model (4.12) represents a two-dimensional Lotka-Volterra model with carrying capacities, which has been discussed by many authors. Such a discussion appears in Freedman (1980) and our main emphasis here is to reconsider all different cases dealt with therein, in the light of

a third species, the mutualist, and to see how the behaviour of solutions change in the presence of the mutualist.

First we list all equilibrium states for the model (4.12). It is easily seen that $E_1(0,0,0)$, $E_2(L_0,0,0)$, $E_3(0,K_1,0)$, $E_4(0,0,K_2)$, $E_5(L_0+\ell K_1,K_1,0)$ and $E_6(L_0,0,K_2)$ are points of equilibria in the feasible octant (first octant) of three dimensional phase space. If the condition

$$(\eta K_1-\delta)(\beta K_2-1) > 0 \tag{4.13}$$

holds, then there exists an equilibrium state $E_7(0,\breve{x}_1,\breve{x}_2)$ in the x_1,x_2 plane, where

$$\breve{x}_1 = \frac{\delta K_1(\beta K_2-1)}{(\beta\eta K_1K_2-\delta)}\,, \qquad \breve{x}_2 = \frac{K_2(\eta K_1-\delta)}{(\beta\eta K_1K_2-\delta)}\,. \tag{4.14}$$

Existence of one or many equilibrium states, interior to the positive octant of the phase space, depends upon the solution of simultaneous equations

$$u - L_0 - \ell x_1 = 0$$

$$1 - \frac{x_1}{K_1} - \frac{\beta x_2}{1+mu} = 0$$

$$\delta\left(1 - \frac{x_2}{K_2}\right) - \eta x_1 = 0$$

If $(\bar{u},\bar{x}_1,\bar{x}_2)$ represents a solution to this system then we can show that $\bar{x}_1$, satisfies the following quadratic equation

$$m\ell\delta\bar{x}_1^2 - \{m\ell\delta K_1+\beta\eta K_1K_2-\delta(1+mL_0)\}\bar{x}_1 - \delta K_1(1+mL_0-\beta K_2) = 0 \qquad (4.15)$$

Case I: $1 + mL_0 = \beta K_2$

In this case, the non-trivial solution of (4.15) is given by

$$\bar{x}_1 = \frac{m\ell\delta K_1+\beta\eta K_1K_2-\delta\beta K_2}{m\ell\delta}$$

or

$$\bar{x}_1 = K_1 - \frac{(\delta-\eta K_1)\beta K_2}{m\ell\delta}\ .$$

$$\text{Then}\quad \bar{x}_2 = \frac{K_2}{\delta}[\delta-\eta\bar{x}_1], \qquad (4.16)$$

$$\text{and}\quad \bar{u} = L_0 + \ell\bar{x}_1.$$

Since K_1 is the carrying capacity of the species x_1, for the biological realization of this equilibrium state we require that $K_1 < \frac{\delta}{\eta}$.

Thus we have shown that if $1 + mL_0 = \beta K_2$ and $K_1 < \frac{\delta}{\eta}$, there exists a unique interior equilibrium $E_8(\bar{u},\bar{x}_1,\bar{x}_2)$, where $\bar{u}$, $\bar{x}_1$ and $\bar{x}_2$ are given by (4.16).

Case II: $1 + mL_0 \neq \beta K_2$

In this case $\bar{x}_1$ is given by

$$\bar{x}_1 = \frac{\mu\pm\sqrt{\mu^2+4m\ell\delta K_1\delta(1+mL_0-\beta K_2)}}{2m\ell\delta} \qquad (4.17)$$

where $\mu = m\ell\delta K_1 + \beta\eta K_1K_2 - \delta(1+mL_0)$. So that depending upon the relative values of the parameters occuring in the model (4.12), we can have one, two or none of the equilibrium states $\in R_+^3$.

We shall denote the interior equilibrium by $E_8(\bar{u},\bar{x}_1,\bar{x}_2)$, if it exists, where $\bar{x}_1$ is given either by the first equation of (4.16) or by (4.17) and $\bar{x}_2$, $\bar{u}$ are always given by

$$\left.\begin{aligned} \bar{x}_2 &= \frac{K_2}{\delta}[\delta-\eta\bar{x}_1] \\ \bar{u} &= L_0 + \ell\bar{x}_1 \end{aligned}\right\} \tag{4.18}$$

We shall now consider the various cases dealt with in Freedman (1980), as mentioned earlier, and observe the effect of introducing the mutualist into the system. For stability analysis, we compute the variational matrix $M(u,x_1,x_2)$ at $(u,x_1,x_2) \in R^3_+$.

$$M(u,x_1,x_2) = \begin{bmatrix} \gamma\left(1-\dfrac{2u}{L_0+\ell x_1}\right) & \dfrac{\gamma\ell u^2}{(L_0+\ell x_1)^2} & 0 \\ \dfrac{m\alpha\beta x_1x_2}{(1+mu)^2} & \alpha\left(1-\dfrac{2x_1}{K_1}\right)-\dfrac{\alpha\beta x_2}{1+mu} & -\dfrac{\alpha\beta x_1}{1+mu} \\ 0 & -\eta x_2 & \delta\left(1-\dfrac{2x_2}{K_2}\right)-\eta x_1 \end{bmatrix} \tag{4.19}$$

<u>Case A:</u> $\frac{1}{\beta} < K_2$, $\frac{\delta}{\eta} < K_1$

In this case the condition (4.13) is satisfied, so that $E_7(0,\tilde{x}_1,\tilde{x}_2)$ exists. It is known that in the absence of the mutualist, there lies a separatrix in the x_1, x_2 plane such that any trajectory of (4.12) initiating on one side of the separatrix approaches E_3 and on the other approached E_4. The equilibrium E_7 lying interior to the plane is found to be unstable. Now we prove the following theorem for (4.12), which highlights the influence of

mutualism on competing species x_1 and x_2.

Theorem 4.4. Let the parameters $m, L_0, \beta, \delta, \eta > 0$ be such that

(a) $\frac{1}{\beta} < K_2$, $\frac{\delta}{\eta} < K_1$

(b) $\exists \mu_1 > 0$ such that

$$1 + mL_0 - \beta K_2 \geq \mu_1 > 0$$

where K_1, $K_2 > 0$ are the carrying capacities of the species x_1 and x_2 respectively. Then

(i) the model (4.12) does not admit any interior equilibrium.

(ii) for every trajectory

$$c^+ = \{(u(t), x_1(t), x_2(t)) : (u(t_0), x_1(t_0), x_2(t_0)) \in R^3_+ ;\ t \geq t_0\},$$

$x_2(t)$ goes to extinction, i.e.

$$\lim_{t\to\infty} x_2(t) = 0$$

Proof: Suppose there exists an interior equilibrium $(\bar{u}, \bar{x}_1, \bar{x}_2) \in R^3_+$, then from (4.18) $\bar{x}_2 > 0 \Rightarrow \bar{x}_1 < \frac{\delta}{\eta}$. $\bar{x}_1$ is given by (4.17), so that

$$0 < \bar{x}_1 < \frac{\delta}{\eta} \Rightarrow \frac{\mu + \sqrt{\mu^2 + 4m\ell\delta K_1 \delta(1 + mL_0 - \beta K_2)}}{2m\ell\delta} < \frac{\delta}{\eta}$$

or $$0 < \sqrt{\mu^2 + 4m\ell\delta K_1 \cdot \delta(1 + mL_0 - \beta K_2)} < \frac{\delta}{\eta} \cdot 2m\ell\delta - \mu$$

Squaring each side and simplifying we get

$$4m\ell\delta K_1\cdot\delta(1+mL_0-\beta K_2) < \frac{\delta^2}{\eta^2}4m^2\ell^2\delta^2 - \frac{\delta}{\eta}\cdot 4m\ell\delta\mu$$

$$\text{or}\quad K_1(1+mL_0-\beta K_2) < \frac{\delta^2}{\eta^2}m\ell - \frac{1}{\eta}\{m\ell\delta K_1+\beta\eta K_1K_2-\delta(1+mL_0)\}$$

$$\text{i.e.}\quad (K_1-\frac{\delta}{\eta})(1+mL_0) < \frac{\delta}{\eta}m\ell(\frac{\delta}{\eta}-K_1)$$

$$\text{or}\quad (K_1-\frac{\delta}{\eta})(1+mL_0+\frac{m\ell\delta}{\eta}) < 0$$

contradiction.

This proves (i). To establish (ii), we consider a function

$$V(x_1,x_2) = (x_1)^{-1/\alpha}\cdot(x_2)^{1/\delta};\quad \alpha>0,\quad x_1,x_2>0 \tag{4.20}$$

and see how does it vary along any trajectory c^+ of the system (4.12). From (4.20)

$$\ell n\{V(x_1,x_2)\} = -\frac{1}{\alpha}\ell n(x_1) + \frac{1}{\delta}\ell n(x_2).$$

Now computing the derivative with respect to t along the trajectory c^+, we get

$$\frac{V'\left(x_1(t),x_2(t)\right)}{V\left(x_1(t),x_2(t)\right)} = -\frac{x_1'(t)}{\alpha x_1(t)} + \frac{x_2'(t)}{\delta x_2(t)}$$

$$= -\left\{1-\frac{x_1(t)}{K_1}-\frac{\beta x_2(t)}{1+mu(t)}\right\} + \left\{1-\frac{x_2(t)}{K_2}-\frac{\eta x_1(t)}{\delta}\right\}$$

from (4.12)

$$= -\left(\frac{\eta}{\delta}-\frac{1}{K_1}\right)x_1(t) - \left(\frac{1}{K_2}-\frac{\beta}{1+mu(t)}\right)x_2(t) \tag{4.21}$$

From (4.12) $u' \geq 0$ for $u \leq L_0 + \ell x_1$, so that for any arbitrarily small $\varepsilon > 0$ there exists a $T \geq t_0$ such that

$$u(t) \geq L_0 - \varepsilon \quad \text{for} \quad t \geq T.$$

Let $0 < \varepsilon \leq \frac{\mu_1}{m}$, then

$$1 + mu(t) \geq 1 + mL_0 - m\varepsilon, \quad t \geq T$$

or
$$\frac{\beta}{1+mu(t)} \leq \frac{\beta}{1+mL_0-m\varepsilon}$$

which gives $\left(\frac{1}{K_2} - \frac{\beta}{1+mu(t)}\right) \geq \left(\frac{1}{K_2} - \frac{\beta}{1+mL_0-m\varepsilon}\right)$

This further implies that

$$\left(\frac{1}{K_2} - \frac{\beta}{1+mu(t)}\right) \geq \left(\frac{1}{K_2} - \frac{\beta}{1+mL_0-\mu_1}\right) \geq 0 \tag{4.22}$$

for $t \geq T$.

Now let us integrate both sides of the equation (4.21) on $[T,t]$. We get

$$\ell n \left\{\frac{V\left(x_1(t),x_2(t)\right)}{V\left(x_1(T),x_2(T)\right)}\right\} = -\int_T^t \left\{\left(\frac{\eta}{\delta} - \frac{1}{K_1}\right) x_1(s) + \left(\frac{1}{K_2} - \frac{\beta}{1+mu(s)}\right) x_2(s)\right\} ds$$

$$\leq -\int_T^t \left\{\left(\frac{\eta}{\delta} - \frac{1}{K_1}\right) x_1(s) + \left(\frac{1}{K_2} - \frac{\beta}{1+mL_0-\mu_1}\right) x_2(s)\right\} ds$$

from (4.22)

which gives

$$V\big(x_1(t),x_2(t)\big) \le V\big(x_1(T),x_2(T)\big)\exp\Big[-\int_T^t\Big\{\Big(\frac{\eta}{\delta}-\frac{1}{K_1}\Big)x_1(s) + \Big(\frac{1}{K_2} - \frac{\beta}{1+mL_0-\mu_1}\Big)x_2(s)\Big\}ds\Big]$$

$$\le V\big(x_1(T),x_2(T)\big)\exp\Big[-\Big(\frac{1}{K_2}-\frac{\beta}{1+mL_0-\mu_1}\Big)\int_T^t x_2(s)ds\Big]$$

from (a). (4.23)

We now claim that the above relation implies $\lim_{t\to\infty} x_2(t) = 0$. If not, then from (4.23) $\lim_{t\to\infty} V\big(x_1(t),x_2(t)\big) = 0$, which again implies that $x_2(t) \to 0$ as $t \to \infty$ because $x_1(t)$ remains bounded. This completes the proof of the theorem (4.4).

Theorem (4.4) shows that the introduction of a mutualist might cause disappearance of the effect of the separatrix, which exists in two dimensions, and also the mutualist-competitor may win all the time. Actually we can show that E_5 is globally asymptotically stable.

Theorem 4.5. Let the conditions of Theorem 4.4 hold. Then the equilibrium state $E_5(L_0+\ell K_1, K_1, 0)$ is globally asymptotically stable in the positive octant of the phase space of the variables u, x_1, x_2.

Proof: From Theorem 4.4, it follows that if $\big(u(t),x_1(t),x_2(t)\big)$ represents a solution to (4.12) with positive initial conditions and defined for all $t \ge t_0 > 0$, then

$$\lim_{t\to\infty} x_2(t) = 0,$$

so that the ω-limit set for any such orbit will lie in the u, x_1 plane.

To establish the theorem, we need to show that E_5 is globally asymptotically stable in the positive quadrant of the u,x_1 plane. However, this follows directly from Theorem 3.3.

Next we consider local stability analysis of all the equilibrium states in Case A.

The eigenvalues of the variational matrix (4.19) evaluated at $E_1(0,0,0)$ are γ,α,δ, so that E_1 is unstable in all directions. Equilibrium state $E_2(L_0,0,0)$ is found to be attracting in the u-direction and repelling in the other two directions. The characteristic values at $E_3(0,K_1,0)$ are $\gamma,-\alpha,\delta-\eta K_1$, so that near E_3, the u-population is increasing but the x_1 and x_2 populations are decreasing. The characteristic roots of the matrix (4.19) at $E_4(0,0,K_2)$ are γ; $\alpha(1-\beta K_2)$, $-\delta$, hence near E_4, u-population is increasing but x_1 and x_2-populations are decreasing. Considering $E_5(L_0+\ell K_1,K_1,0)$, we find that all the characteristic roots (i.e. $-\gamma$, $-\alpha,(\delta-\eta K_1)$) are negative, hence each population is decreasing near E_5. The eigenvalues of the variational matrix at $E_6(L_0,0,K_2)$ are $-\gamma$, $\alpha(1-\frac{\beta K_2}{1+mL_0})$ and $-\delta$. So that E_6 is stable in u and x_2 directions but the stability in the x_1 direction depends upon the magnitude of parameters m and L_0. If the product mL_0 is very small then E_6 is locally asymptotically stable but for larger values of mL_0, E_6 becomes unstable in the x_1 direction. The equilibrium state $E_7(0,\breve{x}_1,\breve{x}_2)$ in the x_1,x_2 plane has eigenvalues $\gamma,\lambda_1,\lambda_2$ where

$$\left.\begin{aligned}\lambda_1 + \lambda_2 &= -\left(\frac{\alpha\tilde{x}_1}{K_1} + \frac{\delta\tilde{x}_2}{K_2}\right)\\ \lambda_1\lambda_2 &= \frac{\alpha}{K_1K_2}(\delta-\beta\eta K_1K_2)\tilde{x}_1\tilde{x}_2 < 0\end{aligned}\right\} \tag{4.24}$$

Thus E_7 continues to be an unstable equilibrium. Now we consider equilibria interior to the positive octant. We have shown in Theorem 4.4 that if the product mL_0 is such that $\beta K_2 < 1 + mL_0$ then there is no interior equilibrium. Also, since $\frac{\delta}{\eta} < K_1$ it makes $\bar{x}_1 > K_1$ in the Case I, so that there is no biologically feasible equilibirum state for $1 + mL_0 = \beta K_2$. In case $\beta K_2 > 1 + mL_0$, we can show that there exists an equilibrium, $E_8(u,\bar{x}_1,\bar{x}_2)$. The variational matrix at any such equilibrium is given by

$$M(\bar{u},\bar{x}_1,\bar{x}_2) = \begin{bmatrix} -\gamma & \gamma\ell & 0 \\ \dfrac{m\alpha\beta\bar{x}_1\bar{x}_2}{(1+m\bar{u})^2} & -\dfrac{\alpha\bar{x}_1}{K_1} & -\dfrac{\alpha\beta\bar{x}_1}{1+m\bar{u}} \\ 0 & -\eta\bar{x}_2 & -\dfrac{\delta\bar{x}_2}{K_2} \end{bmatrix}.$$

The corresponding characteristic equation assumes the following form

$$(-\gamma-\lambda)\left[\left(\frac{\alpha\bar{x}_1}{K_1}+\lambda\right)\left(\frac{\delta\bar{x}_2}{K_2}+\lambda\right) - \frac{\alpha\beta\eta\bar{x}_1\bar{x}_2}{1+m\bar{u}}\right]$$
$$- \frac{m\alpha\beta\bar{x}_1\bar{x}_2}{(1+m\bar{u})^2}\left[\alpha\ell\left(-\frac{\delta\bar{x}_2}{K_2}-\lambda\right)\right] = 0,$$

which can be written as

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0, \tag{4.25}$$

where

$$a_1 = \frac{\alpha\bar{x}_1}{K_1} + \frac{\delta\bar{x}_2}{K_2} + \gamma$$

$$a_2 = \gamma\left(\frac{\alpha\bar{x}_1}{K_1} + \frac{\delta\bar{x}_2}{K_2}\right) + \frac{\alpha\delta\bar{x}_1\bar{x}_2}{K_1K_2} - \frac{\alpha\beta\eta\bar{x}_1\bar{x}_2}{1+m\bar{u}} - \frac{\alpha\beta\gamma m\ell\bar{x}_1\bar{x}_2}{(1+m\bar{u})^2}$$

and

$$a_3 = \gamma\alpha\left[\frac{\delta\bar{x}_1\bar{x}_2}{K_1K_2} - \frac{\beta\eta\bar{x}_1\bar{x}_2}{1+m\bar{u}} - \frac{m\ell\beta\delta\bar{x}_1\bar{x}_2^2}{K_2(1+m\bar{u})^2}\right] \tag{4.26}$$

Rewriting a_3 we have

$$a_3 = \frac{\gamma\alpha\bar{x}_1\bar{x}_2}{K_1K_2(1+m\bar{u})^2}\left[\delta(1+m\bar{u})^2 - \beta\eta K_1K_2(1+m\bar{u}) - m\ell\beta\delta K_1\bar{x}_2\right]$$

$$= \frac{\gamma\alpha\bar{x}_1\bar{x}_2}{K_1K_2(1+m\bar{u})^2}\left[\delta(1+mL_0+m\ell\bar{x}_1)^2 - \beta\eta K_1K_2(1+mL_0+m\ell\bar{x}_1) - m\ell\beta K_1K_2(\delta-\eta x_1)\right]$$

$$= \frac{\gamma\alpha\bar{x}_1\bar{x}_2}{K_1K_2(1+m\bar{u})^2}\left[\delta\{(1+mL_0)^2 + m^2\ell^2x_1^2 + 2m\ell(1+mL_0)\bar{x}_1\} - \beta\eta K_1K_2(1+mL_0) - m\ell\beta\delta K_1K_2\right]$$

$$= \frac{\gamma\alpha\bar{x}_1\bar{x}_2}{K_1K_2(1+m\bar{u})^2}\left[\delta m^2\ell^2\bar{x}_1^2 + (1+mL_0)\{2m\ell\delta\bar{x}_1 + \delta(1+mL_0) - \beta\eta K_1K_2\} - m\ell\beta\delta K_1K_2\right] \tag{4.27}$$

Next we compute

$$a_1a_2-a_3 = \left(\frac{\alpha\bar{x}_1}{K_1} + \frac{\delta\bar{x}_2}{K_2} + \gamma\right)\left[\gamma\left(\frac{\alpha\bar{x}_1}{K_1} + \frac{\delta\bar{x}_2}{K_2}\right) + \frac{\alpha\delta\bar{x}_1\bar{x}_2}{K_1K_2} - \frac{\alpha\beta\eta\bar{x}_1\bar{x}_2}{1+m\bar{u}} - \frac{\alpha\beta\gamma m\ell\bar{x}_1\bar{x}_2}{(1+m\bar{u})^2}\right]$$

$$- \frac{\gamma\alpha\bar{x}_1\bar{x}_2}{K_1K_2(1+m\bar{u})^2}\,[\delta(1+m\bar{u})^2-\beta\eta K_1K_2(1+m\bar{u})-m\ell\delta\beta K_1\bar{x}_2] \tag{4.28}$$

or

$$a_1a_2 - a_3 = b_1\alpha^2 + b_2\alpha + b_3,$$

where

$$b_1 = \frac{\bar{x}_1}{K_1}\left[\frac{\gamma\bar{x}_1}{K_1} + \bar{x}_1\bar{x}_2\left(\frac{\delta}{K_1K_2} - \frac{\beta\eta}{1+m\bar{u}}\right) - \frac{m\ell\beta\gamma\bar{x}_1\bar{x}_2}{(1+m\bar{u})^2}\right]$$

$$b_2 = \frac{2\gamma\delta\bar{x}_1\bar{x}_2}{K_1K_2} + \frac{\gamma^2\bar{x}_1}{K_1} + \frac{\delta\bar{x}_1\bar{x}_2^2}{K_2}\left(\frac{\delta}{K_1K_2} - \frac{\beta\eta}{1+m\bar{u}}\right) - \frac{\gamma^2 m\ell\beta\bar{x}_1\bar{x}_2}{(1+m\bar{u})^2} \tag{4.29}$$

and $$b_3 = \frac{\gamma\delta\bar{x}_2}{K_2}\left(\gamma + \frac{\delta\bar{x}_2}{K_2}\right)$$

As mentioned earlier E_8 exists if $1 + mL_0 < \beta K_2$, and as shown in Theorem 4.4, we can establish that the postive root in the formula (4.17) is not admissible, so that $E_8(u,\bar{x}_1,\bar{x}_2)$ is given by

$$\left.\begin{aligned} \bar{x}_1 &= \frac{\mu-\sqrt{\mu^2-4m\ell\delta K_1\cdot\delta(\beta K_2-1-mL_0)}}{2m\ell\delta}, \\ \bar{u} &= L_0 + \ell\bar{x}_1, \quad \text{and} \quad \bar{x}_2 = \frac{K_2}{\delta}\,[\delta-\eta\bar{x}_1] \end{aligned}\right\} \tag{4.30}$$

where $\mu = m\ell\delta K_1 + \beta\eta K_1K_2 - \delta(1+mL_0)$.

We can show that E_8 is an unstable equilibrium. For this let us consider, relation (4.27) for a_3

$$a_3 = \frac{\gamma\alpha\bar{x}_1\bar{x}_2}{K_1K_2(1+m\bar{u})^2}\,[\delta m^2\ell^2\bar{x}_1^2+(1+mL_0)\{2m\ell\delta\bar{x}_1+\delta(1+mL_0)-\beta\eta K_1K_2\}-m\ell\delta K_1\beta K_2]$$

$$= \frac{\gamma\alpha\bar{x}_1\bar{x}_2}{K_1K_2(1+m\bar{u})^2}\left[\delta m^2\ell^2\bar{x}_1^2+(1+mL_0)\left\{m\ell\delta K_1-\sqrt{\mu^2-4m\ell\delta K_1\delta(\beta K_2-1-mL_0)}\right\}-m\ell\delta K_1\cdot\beta K_2\right]$$

$$= \frac{\gamma\alpha\bar{x}_1\bar{x}_2}{K_1K_2(1+m\bar{u})^2}\left[\delta m^2\ell^2\bar{x}_1^2-m\ell\delta K_1(\beta K_2-1-mL_0)-(1+mL_0)\sqrt{\mu^2-4m\ell\delta K_1\cdot\delta(\beta K_2-1-mL_0)}\right]$$

$$= \frac{\gamma\alpha\bar{x}_1\bar{x}_2}{K_1K_2(1+m\bar{u})^2}\left[\frac{1}{4\delta}\left\{2\mu^2-8m\ell\delta K_1\cdot\delta(\beta K_2-1-mL_0)-2\mu\sqrt{\mu^2-4m\ell\delta K_1\delta(\beta K_2-1-mL_0)}\right\}-(1+mL_0)\sqrt{\mu^2-4m\ell\delta K_1\cdot\delta(\beta K_2-1-mL_0)}\right]$$

$$= \frac{\gamma\alpha\bar{x}_1\bar{x}_2}{K_1K_2(1+m\bar{u})^2}\left[-\frac{\sqrt{\mu^2-4m\ell\delta K_1\delta(\beta K_2-1-mL_0)}}{2\delta}\left\{\mu-\sqrt{\mu^2-4m\ell\delta K_1\delta(\beta K_2-1-mL_0)}\right\}-(1+mL_0)\sqrt{\mu^2-4m\ell\delta K_1\delta(\beta K_2-1-mL_0)}\right]$$

$$< 0.$$

Using the Routh-Hurwitz criterion, we find that E_8 is unstable. This proves the following theorem.

Theorem 4.6. Let the parameters $m, L_0, \beta, \delta, \eta > 0$ be such that

(i) $\frac{1}{\beta} < K_2$, $\frac{\delta}{\eta} < K_1$,

(ii) $1 + mL_0 < \beta K_2$

(iii) $\mu > \sqrt{4m\ell\delta K_1 \cdot \delta(\beta K_2 - 1 - mL_0)}$,

where $K_1, K_2 > 0$ are the carrying capacities of the species x_1 and x_2 respectively and $\mu = m\ell\delta K_1 + \beta\eta K_1 K_2 - \delta(1+mL_0)$. Then there exists a biologically feasible interior equilibrium state $E_8(\bar{u},\bar{x}_1,\bar{x}_2)$, which is unstable.

The table T_A, given below summarises main features of the Case A.

T_A. $\frac{1}{\beta} < K_2$, $\frac{\delta}{\eta} < K_1$

equilibria	u-direction	x_1-direction	x_2-direction
$E_1(0,0,0)$	unstable	unstable	unstable
$E_2(L_0,0,0)$	stable	unstable	unstable
$E_3(0,K_1,0)$	unstable	stable	stable
$E_4(0,0,K_2)$	unstable	stable	stable
$E_5(L_0+\ell K_1,K_1,0)$	stable	stable	stable
$E_6(L_0,0,K_2)$	stable	$\begin{cases} \text{stable if } 1+mL_0 \leq \beta K_2 \\ \text{unstable if } 1+mL_0 > \beta K_2 \end{cases}$	stable
$E_7(0,\breve{x}_1,\breve{x}_2)$	unstable	Hyperbolic point in the x_1x_2 plane.	
$E_8(\bar{u},\bar{x}_1,\bar{x}_2)$	$\begin{cases} 1+mL_0 \geq \beta K_2, \\ 1+mL_0 < \beta K_2, \end{cases}$	there is no interior equilibrium E_8 exists and is unstable.	

<u>Case B</u>: $K_2 < \frac{1}{\beta}$, $K_1 < \frac{\delta}{\eta}$

The condition (4.13) is satisfied, so that there exists an equilibrium $E_7(0,\breve{x}_1,\breve{x}_2)$ in the x_1,x_2 plane. It is known that in

the absence of the mutualist the interior equilibrium in the x_1x_2 plane is a stable attractor in the positive quadrant of the plane.

We find that in this case, the mutualist does not seem to cause any change in the stability behaviour. Local stability of various equilibria is listed below in Table T_B.

T_B

equilibria	u-direction	x_1-direction	x_2-direction
$E_1(0,0,0)$	unstable	unstable	unstable
$E_2(L_0,0,0)$	stable	unstable	unstable
$E_3(0,K_1,0)$	unstable	stable	unstable
$E_4(0,0,K_2)$	unstable	unstable	stable
$E_5(L_0+\ell K_1,K_1,0)$	stable	stable	unstable
$E_6(L_0,0,K_2)$	stable	unstable	stable
$E_7(0,\overset{\frown}{x}_1,\overset{\frown}{x}_2)$	unstable	stable	stable
$E_8(u,\bar{x}_1,\bar{x}_2)$	stable	stable	stable

The verification of the above list follows easily from the discussion of the Section A, except for the last case. So, we consider $E_8(\bar{u},\bar{x}_1,\bar{x}_2)$.

From (4.17), $\bar{u},\bar{x}_1,\bar{x}_2$ are given by

$$\bar{x}_1 = \frac{\mu+\sqrt{\mu^2+4m\ell\delta K_1\cdot\delta(1+mL_0-\beta K_2)}}{2m\ell\delta}$$

where $\mu = m\ell\delta K_1 + \beta\eta K_1K_2 - \delta(1+mL_0)$

$$\bar{x}_2 = \frac{K_2}{\delta}[\delta - \eta\bar{x}_1]$$

$$\bar{u} = L_0 + \ell\bar{x}_1. \tag{4.31}$$

It can be shown $\bar{x}_1 < K_1 < \frac{\delta}{\eta}$, so that E_8 is biologically feasible. Now we need to show that $a_1 > 0$, $a_3 > 0$ and $a_1a_2 - a_3 > 0$, where a_1, a_2, a_3 are given by (4.26).

$$a_1 = \frac{\alpha\bar{x}_1}{K_1} + \frac{\delta\bar{x}_2}{K_2} + \gamma > 0$$

and $$a_3 = \frac{\gamma\alpha\bar{x}_1\bar{x}_2}{K_1K_2(1+m\bar{u})^2}[\delta m^2\ell^2\bar{x}_1^2 + (1+mL_0)\{2m\ell\delta\bar{x}_1 + \delta(1+mL_0) - \beta\eta K_1K_2\} - m\ell\delta K_1 \cdot \beta K_2]$$

from (4.27).

Now from (4.31)

$$2m\ell\delta\bar{x}_1 + \delta(1+mL_0) - \beta\eta K_1K_2 = m\ell\delta K_1 + \sqrt{\mu^2 + 4m\ell\delta K_1 \cdot \delta(1+mL_0 - \beta K_2)}$$

Multiply both sides by $(1+mL_0)$ and then subtract $m\ell\delta K_1 \cdot \beta K_2$ from both the sides to get

$$(1+mL_0)\{2m\ell\delta\bar{x}_1 + \delta(1+mL_0) - \beta\eta K_1K_2\} - m\ell\delta K_1 \cdot \beta K_2$$

$$= m\ell\delta K_1(1+mL_0-\beta K_2) + (1+mL_0)\sqrt{\mu^2 + 4m\ell\delta K_1 \cdot \delta(1+mL_0-\beta K_2)} > 0.$$

This implies that $a_3 > 0$. Next we consider $(a_1a_2 - a_3)$. From (4.28)

$$a_1a_2-a_3 = \left(\frac{\alpha\bar{x}_1}{K_1}+\frac{\delta\bar{x}_2}{K_2}+\gamma\right)\left[\frac{\gamma\alpha\bar{x}_1}{\delta K_1(1+m\bar{u})^2}\{\delta(1+m\bar{u})^2-\beta m\ell\delta K_1\bar{x}_2\} + \frac{\gamma\delta\bar{x}_2}{K_2}\right.$$

$$\left. + \frac{\alpha\bar{x}_1\bar{x}_2}{K_1K_2(1+m\bar{u})}\{\delta(1+m\bar{u})-\beta\eta K_1K_2\}\right]$$

$$- \frac{\gamma\alpha\bar{x}_1\bar{x}_2}{K_1K_2(1+m\bar{u})^2}[\delta m^2\ell^2\bar{x}_1^2+(1+mL_0)\{2m\ell\delta\bar{x}_1+\delta(1+mL_0)-\beta\eta K_1K_2\}$$

$$-m\ell\delta K_1\cdot\beta K_2], \qquad \text{using (4.27) also.}$$

$$= \left(\frac{\alpha\bar{x}_1}{K_1}+\frac{\delta\bar{x}_2}{K_2}+\gamma\right)\left[\frac{\gamma\alpha\bar{x}_1}{\delta K_1(1+m\bar{u})^2}\{\delta m^2\ell^2\bar{x}_1^2+(1+mL_0)(2m\ell\delta\bar{x}_1+\delta(1+mL_0)).\right.$$

$$\left.-m\ell\delta K_1\cdot\beta K_2+m\ell\eta K_1\beta K_2\bar{x}_1\} + \frac{\gamma\delta\bar{x}_2}{K_2} + \frac{\alpha\bar{x}_1\bar{x}_2}{K_1K_2(1+m\bar{u})}\{\delta(1+m\bar{u})-\beta\eta K_1K_2\}\right]$$

$$- \frac{\gamma\alpha\bar{x}_1\bar{x}_2}{K_1K_2(1+m\bar{u})^2}[\delta m^2\ell^2\bar{x}_1^2+(1+mL_0)\{2m\ell\delta\bar{x}_1+\delta(1+mL_0)-\beta\eta K_1K_2\}$$

$$-m\ell\delta K_1\cdot\beta K_2]$$

$$= \frac{\delta m^2\ell^2\bar{x}_1^2\cdot\gamma\alpha\bar{x}_1}{K_1(1+m\bar{u})^2}\left\{\frac{1}{\delta}\left(\frac{\alpha\bar{x}_1}{K_1}+\frac{\delta\bar{x}_2}{K_2}+\gamma\right) - \frac{\bar{x}_2}{K_2}\right\}$$

$$+ \frac{\gamma\alpha\bar{x}_1}{K_1(1+m\bar{u})^2}\left[\frac{1}{\delta}\left(\frac{\alpha\bar{x}_1}{K_1}+\frac{\delta\bar{x}_2}{K_2}+\gamma\right)\{(1+mL_0)(2m\ell\delta\bar{x}_1+\delta(1+mL_0))\right.$$

$$-m\ell\delta K_1\beta K_2+m\ell\eta K_1\beta K_2\bar{x}_1\} - \frac{\bar{x}_2}{K_2}\{(1+mL_0)(2m\ell\delta\bar{x}_1+\delta(1+mL_0)-\beta\eta K_1K_2)$$

$$\left.-m\ell\delta K_1\cdot\beta K_2\}\right] + \left(\frac{\alpha\bar{x}_1}{K_1}+\frac{\delta\bar{x}_2}{K_2}+\gamma\right)\left[\frac{\gamma\delta\bar{x}_2}{K_2}+\frac{\alpha\bar{x}_1\bar{x}_2}{K_1K_2(1+m\bar{u})}\{\delta(1+m\bar{u})-\beta\eta K_1K_2\}\right]$$

$$= \frac{\delta m^2\ell^2\bar{x}_1^2\cdot\gamma\alpha\bar{x}_1}{K_1(1+m\bar{u})^2}\left\{\frac{1}{\delta}\left(\frac{\alpha\bar{x}_1}{K_1}+\gamma\right)\right\} + \frac{\gamma\alpha\bar{x}_1}{K_1(1+m\bar{u})^2}\left[\left\{(1+mL_0)(2m\ell\delta\bar{x}_1+\delta(1+mL_0))\right.\right.$$

$$-m\ell\delta K_1\cdot\beta K_2\Big\}\cdot\Big\{\frac{1}{\delta}\left(\frac{\alpha\bar{x}_1}{K_1}+\frac{\delta\bar{x}_2}{K_2}+\gamma\right)-\frac{\bar{x}_2}{K_2}\Big\}$$

$$+\frac{1}{\delta}\left(\frac{\alpha\bar{x}_1}{K_1}+\frac{\delta\bar{x}_2}{K_2}+\gamma\right)m\ell\eta K_1\beta K_2\bar{x}_1+\frac{\bar{x}_2}{K_2}(1+mL_0)\beta\eta K_1K_2\Big]$$

$$> 0$$

because $2m\ell\delta\bar{x}_1+\delta(1+mL_0)-m\ell\delta K_1\cdot\beta K_2 > 2m\ell\delta\bar{x}_1+\delta(1+mL_0)-m\ell\delta K_1,$

$\beta K_2 < 1$

$$= \beta\eta K_1K_2+\sqrt{\mu^2+4m\ell\delta K_1\cdot\delta(1+mL_0-\beta K_2)}$$

from (4.31)

$$> 0.$$

Thus we have shown that $a_1 > 0$, $a_3 > 0$ and $a_1a_2 - a_3 > 0$. This justifies the last line of the Table T.

This analysis shows that the introduction of the mutualist into the competitive system does not affect the stability behaviour of the interior equilibrium states; it only changes the equilibrium populations. Biologically, it means that the effect of the species x_2 on the species x_1 is already so small that lowering it down further by the presence of the mutualist does not create any drastic change in the behaviour of the system.

<u>Case C</u>: $\frac{1}{\beta} < K_2$, $K_1 < \frac{\delta}{\eta}$.

It is known that for the competitive system (i.e. in the absence of the mutualist) the equilibrium $E_4(0,0,K_2)$ is stable and all solutions initiating in the interior of the positive quadrant tend to E_4.

In this case the condition (4.13) is not satisfied, so that E_7 does not exist, i.e. there is no equilibrium state interior to the positive quadrant of x_1, x_2 plane.

We can show, as in the previous cases, that in this case $E_1(0,0,0)$ is unstable in all directions, $E_2(L_0,0,0)$ is stable in the u direction but unstable in other directions, $E_3(0,K_1,0)$ is stable in the x_1 direction but unstable in the other two directions, $E_4(0,0,K_2)$ is unstable in the u-direction but stable in the x_1 and x_2 directions, $E_5(L_0+K_1,K_1,0)$ is stable in the u and x_1 directions but unstable in the x_2 direction, $E_6(L_0,0,K_2)$ is stable in the u and x_2 directions but the stability in the x_1-direction depends on the sign of $(1-\frac{\beta K_2}{1+mL_0})$, E_7 does not exist. Here again, we see that the mutualist will affect the stability of E_6.

If $1 + mL_0 \leq \beta K_2$, E_6 is stable in all three directions and if $1 + mL_0 > \beta K_2$ E_6 becomes unstable in the x_1 direction. Also as mentioned earlier, the competitive system alone does not admit any interior equilibria but we shall show that by the help of the mutualist it is possible to have interior equilibria. The interior equilibria are given by (4.16) and (4.17).

<u>Case C_1:</u> $1 + mL_0 \geq \beta K_2$.

In this case, we get only one interior equilibrium state $E_8(\bar{u},\bar{x}_1,\bar{x}_2)$ where

$$\bar{x}_1 = \frac{\mu+\sqrt{\mu^2+4m\ell\delta K_1\cdot\delta(1+mL_0-\beta K_2)}}{2m\ell\delta}$$

where $\mu = m\ell\delta K_1 + \beta\eta K_1K_2 - \delta(1+mL_0)$

$$\bar{x}_2 = \frac{K_2}{\delta}[\delta-\eta\bar{x}_1]$$

$$\bar{u} = L_0 + \ell\bar{x}_1$$

It can be shown that $\bar{x}_1 < K_1 < \frac{\delta}{\eta}$. By a similar calculation, as done in Case B, we can show that E_8, in this case, is asymptotically stable (locally).

<u>Case C_2:</u> $1 + mL_0 < \beta K_2$.

From (4.17)

$$\bar{x}_1 = \frac{\mu \pm \sqrt{\mu^2 - 4m\ell\delta K_1 \cdot \delta(\beta K_2 - 1 - mL_0)}}{2m\ell\delta}$$

To make this feasible we impose the condition

$$\mu \geq \sqrt{4m\ell\delta K_1 \cdot \delta(\beta K_2 - 1 - mL_0)} \tag{4.32}$$

Now, we are going to show that the equilibrium corresponding to

$$\bar{x}_1 = \frac{\mu + \sqrt{\mu^2 - 4m\ell\delta K_1 \cdot \delta(\beta K_2 - 1 - mL_0)}}{2m\ell\delta} \tag{4.33}$$

is always asymptotically stable. For this we shall establish that a_1, a_3 and $a_1a_2 - a_3$ are positive, where a_1, a_2, a_3 are given by (4.26).

$$a_1 = \frac{\alpha\bar{x}_1}{K_1} + \frac{\delta\bar{x}_2}{K_2} + \gamma > 0$$

From (4.27)

$$a_3 = \frac{\gamma\alpha\bar{x}_1\bar{x}_2}{K_1K_2(1+m\bar{u})^2}[\delta m^2\ell^2\bar{x}_1^2+(1+mL_0)\{2m\ell\delta\bar{x}_1+\delta(1+mL_0)-\beta\eta K_1K_2\}-m\ell\delta K_1\cdot\beta K_2]$$

$$= \frac{\gamma\alpha\bar{x}_1\bar{x}_2}{K_1K_2(1+m\bar{u})^2}\Big[\delta m^2\ell^2\bar{x}_1^2+(1+mL_0)\Big\{m\ell\delta K_1+\sqrt{\mu^2-4m\ell\delta K_1\delta(\beta K_2-1-mL_0)}\Big\} -m\ell\delta K_1\cdot\beta K_2\Big]$$

using (4.33) and (4.17).

$$= \frac{\gamma\alpha\bar{x}_1\bar{x}_2}{K_1K_2(1+m\bar{u})^2}\Big[\delta m^2\ell^2\bar{x}_1^2-m\ell\delta K_1(\beta K_2-1-mL_0) +(1+mL_0)\sqrt{\mu^2-4m\ell\delta K_1\delta(\beta K_2-1-mL_0)}\Big]$$

$$> 0 \quad \text{because} \quad \bar{x}_1 > \frac{\mu}{2m\ell\delta} \geq \frac{\sqrt{4m\ell\delta K_1\cdot\delta(\beta K_2-1-mL_0)}}{2m\ell\delta}$$

$$\text{or} \quad \bar{x}_1^2 > \frac{K_1}{m\ell}(\beta K_2-1-mL_0)$$

$$\text{i.e.} \quad \delta m^2\ell^2\bar{x}_1^2 > \delta m\ell K_1(\beta K_2-1-mL_0). \tag{4.34}$$

Now we consider $(a_1a_2-a_3)$. From (4.28)

$$a_1a_2 - a_3 = \left(\frac{\alpha\bar{x}_1}{K_1}+\frac{\delta\bar{x}_2}{K_2}+\gamma\right)\left[\frac{\gamma\delta\bar{x}_2}{K_2}+\alpha\left\{\frac{\gamma\bar{x}_1}{K_1}+\frac{\delta\bar{x}_1\bar{x}_2}{K_1K_2}-\frac{\beta\eta\bar{x}_1\bar{x}_2}{1+m\bar{u}}-\frac{\beta m\gamma\ell\bar{x}_1\bar{x}_2}{(1+m\bar{u})^2}\right\}\right]$$
$$-\gamma\alpha\bar{x}_1\bar{x}_2\left[\frac{\delta}{K_1K_2}-\frac{\beta\eta}{1+m\bar{u}}-\frac{m\ell\delta\beta\bar{x}_2}{K_2(1+m\bar{u})^2}\right]$$

or

$$a_1a_2 - a_3 = b_1\alpha^2 + b_2\alpha + b_3 \tag{4.35}$$

where

$$b_1 = \frac{\bar{x}_1}{K_1}\left[\frac{\gamma\bar{x}_1}{K_1} + \bar{x}_1\bar{x}_2\left\{\frac{\delta}{K_1K_2} - \frac{\beta\eta}{1+m\bar{u}}\right\} - \frac{\beta m\gamma\ell\bar{x}_1\bar{x}_2}{(1+m\bar{u})^2}\right]$$

$$b_2 = \left(\frac{\delta\bar{x}_2}{K_2} + \gamma\right)\left\{\frac{\gamma\bar{x}_1}{K_1} + \frac{\delta\bar{x}_1\bar{x}_2}{K_1K_2} - \frac{\beta\eta\bar{x}_1\bar{x}_2}{1+m\bar{u}} - \frac{\beta m\gamma\ell\bar{x}_1\bar{x}_2}{(1+m\bar{u})^2}\right\} - \gamma\bar{x}_1\bar{x}_2\left[-\frac{\beta\eta}{1+m\bar{u}} - \frac{m\ell\delta\beta\bar{x}_2}{K_2(1+m\bar{u})^2}\right]$$

$$= \left(\frac{\delta\bar{x}_2}{K_2} + \gamma\right)\cdot\frac{b_1K_1}{\bar{x}_1} + \gamma\bar{x}_1\bar{x}_2\left[\frac{\beta\eta}{1+m\bar{u}} + \frac{m\ell\delta\beta\bar{x}_2}{K_2(1+m\bar{u})^2}\right]$$

and

$$b_3 = \frac{\gamma\delta\bar{x}_2}{K_2}\left(\gamma + \frac{\delta\bar{x}_2}{K_2}\right).$$

We notice that if $b_1 > 0$ then $b_2 > 0$, which makes $a_1a_2 - a_3 > 0$. So that let us consider b_1 again.

$$b_1 = \frac{\bar{x}_1}{K_1}\left[\frac{\gamma\bar{x}_1}{K_1}\{(1+m\bar{u})^2 - m\ell\beta K_1\bar{x}_2\} + \frac{\bar{x}_1\bar{x}_2}{K_1K_2}\{\delta(1+m\bar{u}) - \beta\eta K_1K_2\}\right] \tag{4.36}$$

Consider

$$(1+m\bar{u})^2 - m\ell\beta K_1\bar{x}_2$$

$$= (1+mL_0+m\ell\bar{x}_1)^2 - m\ell\beta K_1\cdot\frac{K_2}{\delta}(\delta-\eta\bar{x}_1)$$

$$= \frac{1}{\delta}[\delta(1+mL_0)^2 + \delta m^2\ell^2\bar{x}_1^2 + 2m\ell\delta(1+mL_0)\bar{x}_1 - m\ell\beta K_1K_2\delta + m\ell\beta K_1K_2\eta\bar{x}_1]$$

$$= \frac{1}{\delta}[\delta m^2\ell^2\bar{x}_1^2 + (1+mL_0)\{2m\ell\delta\bar{x}_1 + \delta(1+mL_0)\} - m\ell\delta K_1\cdot\beta K_2 + m\ell\beta K_1K_2\eta\bar{x}_1]$$

$$= \frac{1}{\delta}[\delta m^2\ell^2\bar{x}_1^2 + (1+mL_0)\{2m\ell\delta\bar{x}_1 + \delta(1+mL_0) - m\ell\delta K_1\} + (1+mL_0)m\ell\delta K_1$$
$$- m\ell\delta K_1\beta K_2 + m\ell\beta K_1K_2\eta\bar{x}_1]$$

$$= \frac{1}{\delta}[\{\delta m^2\ell^2\bar{x}_1^2 - m\ell\delta K_1(\beta K_2 - 1 - mL_0)\} + (1+mL_0)\{2m\ell\delta\bar{x}_1 + \delta(1+mL_0) - m\ell\delta K_1\} +$$

$$+m\ell\beta K_1K_2\eta\bar{x}_1] > 0 \quad \text{using (4.33) and (4.34).} \tag{4.37}$$

Next consider

$$\begin{aligned}\delta(1+m\bar{u}) - \beta\eta K_1K_2 &= \delta(1+mL_0+m\ell\bar{x}_1) - \beta\eta\, K_1K_2 \\ &= m\ell\delta\bar{x}_1 + \delta(1+mL_0) - \beta\eta K_1K_2 \\ &= \frac{m\ell\delta K_1+\beta\eta K_1K_2-\delta(1+mL_0)}{2} + \frac{1}{2}\sqrt{\mu^2-4m\ell\delta K_1\cdot\delta(\beta K_2-1-mL_0)} \\ &\quad + \delta(1+mL_0)-\beta\eta K_1K_2 \quad \text{from (4.33)} \\ &= \frac{m\ell\delta K_1-\beta\eta K_1K_2+\delta(1+mL_0)}{2} + \frac{1}{2}\sqrt{\mu^2-4m\ell\delta K_1\cdot\delta(\beta K_2-1-mL_0)}\end{aligned} \tag{4.38}$$

Since we are interested in equilibria for which $\bar{x}_1 \leq K_1$, so that $\frac{\mu}{2m\ell\delta} < K_1$ or $m\ell\delta K_1 + \beta\eta K_1K_2 - \delta(1+mL_0) < 2m\ell\delta K_1$, which implies that $m\ell\delta K_1 - \beta\eta K_1K_2 + \delta(1+mL_0) > 0$. Hence from (4.38) we find that $\delta(1+m\bar{u}) - \beta\eta K_1K_2 > 0$. Now combining (4.37), (4.38) and (4.36), we show that $b_1 > 0$. As discussed earlier $b_1 > 0 \Rightarrow b_2 > 0$ and b_3 is always positive, so that using the Routh-Hurwitz criterion, the equilibrium is asymptotically stable.

Next we consider the equilibrium

$$\bar{u} = L_0 + \bar{x}_1, \quad \bar{x}_1 = \frac{\mu - \sqrt{\mu^2-4m\ell\delta K_1\cdot\delta(\beta K_2-1-mL_0)}}{2m\ell\delta}, \quad \bar{x}_2 = \frac{K_2}{\delta}[\delta-\eta\bar{x}_1].$$

Similar computation, as done in previous cases, shows that for this equilibrium $a_3 < 0$. Hence the equilibrium state is unstable.

A summary of the Case C is given in Table T_c.

T_c: $\frac{1}{\beta} < K_2$, $K_1 < \frac{\delta}{\eta}$.

equilibria	u-direction	x_1-direction	x_2-direction
$E_1(0,0,0)$	unstable	unstable	unstable
$E_2(L_0,0,0)$	stable	unstable	unstable
$E_3(0,K_1,0)$	unstable	stable	unstable
$E_4(0,0,K_2)$	unstable	stable	stable
$E_5(L_0+\ell K_1,K_1,0)$	stable	stable	unstable
$E_6(L_0,0,K_2)$	stable	if $1+mL_0 \leq \beta K_2$ stable if $1+mL_0 > \beta K_2$ unstable	stable
$E_7(0,\tilde{x}_1,\tilde{x}_2)$	does not exist		
$E_8(\bar{u},\bar{x}_1,\bar{x}_2)$	$1+mL_0 \geq \beta K_2$ $1+mL_0 < \beta K_2$	asymptotically stable. one stable and another unstable.	

Case D: $K_2 < \frac{1}{\beta}$, $\frac{\delta}{\eta} < K_1$

In two dimensions (i.e. in the absence of the mutualist) it is known that all solutions initiating in the interior of the first quadrant tend towards the equilibrium on the x_1-axis i.e. $(K_1,0)$.

We shall show that in this case, there is no interior equilibrium in the positive octant and also that all solutions initiating in the interior of the positive octant approach $E_5(L_0+\ell K_1,K_1,0)$. We state the following result.

Theorem 4.7. Let the parameters $\beta,\delta,\eta > 0$ be such that $K_2 < \frac{1}{\beta}$ and $\frac{\delta}{\eta} < K_1$, where $K_1,K_2 > 0$ are the carrying capacities of the species x_1 and x_2 respectively. Then for every trajectory

$$c^+ = \{(u(t), x_1(t), x_2(t)) : (u(t_0), x_1(t_0), x_2(t_0)) \in R^3_+;\ t \geq t_0 > 0\},$$

$x_2(t)$ goes to extinction and the equilibrium state $E_5(L_0 + K_1, K_1, 0)$ is globally asymptotically stable in the positive octant of the phase space of the variables u, x_1, x_2.

Proof: The proof runs parallel to the Theorems 4.4 and 4.5. We can show that there is no interior equilibrium in this case, as proved in Theorem 4.4. Then by considering a function

$$V(x_1, x_2) = (x_1)^{-1/\alpha} \cdot (x_2)^{1/\delta}; \quad x_1, x_2 > 0, \quad \alpha > 0$$

and computing its derivative along the solutions of (4.12), we prove that $\lim_{t\to\infty} x_2(t) = 0$. As in (4.21)

$$\begin{aligned}\frac{V'(x_1(t), x_2(t))}{V(x_1(t), x_2(t))} &= -\left(\frac{\eta}{\delta} - \frac{1}{K_1}\right) x_1(t) - \left(\frac{1}{K_2} - \frac{\beta}{1+mu(t)}\right) x_2(t) \\ &\leq -\left(\frac{1}{K_2} - \frac{\beta}{1+mu(t)}\right) x_2(t) \\ &\leq -\left(\frac{1}{K_2} - \beta\right) x_2(t)\end{aligned}$$

or integrating on the interval $[t_0, t]$, we get

$$V(x_1(t), x_2(t)) \leq V(x_1(t_0), x_2(t_0)) \exp\left[-\left(\frac{1}{K_2} - \beta\right) \int_{t_0}^{t} x_2(s) ds\right].$$

From this we conclude that $\lim_{t\to\infty} V(x_1(t), x_2(t)) = 0$, which implies that $\lim_{t\to\infty} x_2(t) = 0$, because $x_1(t)$ remains bounded.

The global asymptotic stability of E_5 is established exactly

the same way was in Theorem 4.5. This completes the proof of the Theorem 4.7.

□

In this case the role of the mutualist is not that important. Conditions are such that the species x_1 is already in a dominating position, so that the mutualist just enhances this dominance. Other equilibria and their stability as listed in the Table T_D.

T_D. $K_2 < \frac{1}{\beta}$, $\frac{\delta}{\eta} < K_1$

equilibria	u-direction	x_1-direction	x_2-direction
$E_1(0,0,0)$	unstable	unstable	unstable
$E_2(L_0,0,0)$	stable	unstable	unstable
$E_3(0,K_1,0)$	unstable	stable	stable
$E_4(0,0,K_2)$	unstable	unstable	stable
$E_5(L_0+\ell K_1,K_1,0)$	stable	stable	stable
$E_6(L_0,0,K_2)$	stable	unstable	stable
$E_7(0,\breve{x}_1,\breve{x}_2)$	does not exist		
$E_8(\bar{u},\bar{x}_1,\bar{x}_2)$	does not exist		

4.7. Periodic Solutions.

In this section, we use the Hopf-Bifurcation theorem to establish that an ecological system, which is modelled by the general system (4.1), can exhibit small amplitude oscillations if the functions h, g_1, g_2, q_1 and q_2 satisfy a certain set of conditions.

Let us assume that $(\bar{u}, \bar{x}_1, \bar{x}_2)$ is an equilibrium state for the system (4.1), interior to the positive octant of the three dimensional phase space. $\bar{u}$, $\bar{x}_1$, $\bar{x}_2$ are given by

$$\left.\begin{aligned} \bar{u} &= L(\bar{x}_1) \\ g_1\big(\bar{x}_1, L(\bar{x}_1)\big) &= q_1\big(\bar{x}_1, \bar{x}_2, L(\bar{x}_1)\big) \\ g_2(\bar{x}_2) &= q_2(\bar{x}_1, \bar{x}_2) \end{aligned}\right\} \tag{4.39}$$

The characteristic values of the variational matrix, evaluated at $(\bar{u}, \bar{x}_1, \bar{x}_2)$ are given by the following equation, which is obtained from (4.2)

$$\begin{vmatrix} \bar{u}h_u(\bar{u},\bar{x}_1)-\lambda & \bar{u}h_{x_1}(\bar{u},\bar{x}_1) & 0 \\ \begin{array}{l}\alpha\bar{x}_1\{g_{1u}(\bar{x}_1,\bar{u}) \\ \quad -q_{1u}(\bar{x}_1,\bar{x}_2,\bar{u})\}\end{array} & \begin{array}{l}\alpha x_1\{g_{1x_1}(\bar{x}_1,\bar{u}) \\ \quad -q_{1x_1}(\bar{x}_1,\bar{x}_2,\bar{u})\}-\lambda\end{array} & -\alpha\bar{x}_1 q_{1x_2}(\bar{x}_1,\bar{x}_2,\bar{u}) \\ 0 & -\bar{x}_2 q_{2x_1}(\bar{x}_1,\bar{x}_2) & \begin{array}{l}\bar{x}_2\{g_{2x_2}(\bar{x}_2) \\ \quad -q_{2x_2}(\bar{x}_1,\bar{x}_2)\}-\lambda\end{array} \end{vmatrix} = 0$$

when expanded this assumes the form

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0 \tag{4.40}$$

where

$$a_1 = -[\bar{u}h_u(\bar{u},\bar{x}_1)+\alpha\bar{x}_1\{g_{1x_1}(\bar{x}_1,\bar{u})-q_{1x_1}(\bar{x}_1,\bar{x}_2,\bar{u})\}+\bar{x}_2\{g_{2x_2}(\bar{x}_2)-q_{2x_2}(\bar{x}_1,\bar{x}_2)\}]$$

$$a_2 = \bar{u}h_u(\bar{u},\bar{x}_1)[\alpha\bar{x}_1\{g_{1x_1}(\bar{x}_1,\bar{u})-q_{1x_1}(\bar{x}_1,\bar{x}_2,\bar{u})\}+\bar{x}_2\{g_{2x_2}(\bar{x}_2)-q_{2x_2}(\bar{x}_1,\bar{x}_2)\}]$$
$$+ \alpha\bar{x}_1\bar{x}_2[\{g_{1x_1}(\bar{x}_1,\bar{u})-q_{1x_1}(\bar{x}_1,\bar{x}_2,\bar{u})\}\cdot\{g_{2x_2}(\bar{x}_2)-q_{2x_2}(\bar{x}_1,\bar{x}_2)\}$$
$$-q_{1x_2}(\bar{x}_1,\bar{x}_2,\bar{u})q_{2x_1}(\bar{x}_1,\bar{x}_2)] - \alpha\bar{u}\bar{x}_1h_{x_1}(\bar{u},\bar{x}_1)[g_{1u}(\bar{x}_1,\bar{u})-q_{1u}(\bar{x}_1,\bar{x}_2,\bar{u})]$$

and

$$a_3 = -\alpha\bar{u}\bar{x}_1\bar{x}_2[h_u(\bar{u},\bar{x}_1)\{(g_{1x_1}(\bar{x}_1,\bar{u})-q_{1x_1}(\bar{x}_1,\bar{x}_2,\bar{u}))(g_{2x_2}(\bar{x}_2)-q_{2x_2}(\bar{x}_1,\bar{x}_2))$$
$$-q_{1x_2}(\bar{x}_1,\bar{x}_2,\bar{u})\cdot q_{2x_1}(\bar{x}_1,\bar{x}_2)\} - h_{x_1}(\bar{u},\bar{x}_1)\{g_{1u}(\bar{x}_1,\bar{u})-q_{1u}(\bar{x}_1,\bar{x}_2,\bar{u})\}$$
$$\cdot\{g_{2x_2}(\bar{x}_2)-q_{2x_2}(\bar{x}_1,\bar{x}_2)\}]$$

We now compute $a_1a_2 - a_3$ and express it as a polynomial in α.

$$a_1a_2 - a_3 = b_1\alpha^2 + b_2\alpha + b_3 \tag{4.41}$$

where

$$b_1 = -\bar{u}\bar{x}_1^2h_u(\bar{u},\bar{x}_1)\{g_{1x_1}(\bar{x}_1,\bar{u})-q_{1x_1}(\bar{x}_1,\bar{x}_2,\bar{u})\}^2$$
$$+ \bar{u}\bar{x}_1^2h_{x_1}(\bar{u},\bar{x}_1)\{g_{1x_1}(\bar{x}_1,\bar{u})-q_{1x_1}(\bar{x}_1,\bar{x}_2,\bar{u})\}\{g_{1u}(\bar{x}_1,\bar{u})-q_{1u}(\bar{x}_1,\bar{x}_2,\bar{u})\}$$
$$- \bar{x}_1^2\bar{x}_2\{g_{1x_1}(\bar{x}_1,\bar{u})-q_{1x_1}(\bar{x}_1,\bar{x}_2,\bar{u})\}[\{\bar{g}_{1x_1}(\bar{x}_1,\bar{u})-q_{1x_1}(\bar{x}_1,\bar{x}_2,\bar{u})\}$$
$$\cdot\{g_{2x_2}(\bar{x}_2)-q_{2x_2}(\bar{x}_1,\bar{x}_2)\}-q_{1x_2}(\bar{x}_1,\bar{x}_2,\bar{u})\cdot q_{2x_1}(\bar{x}_1,\bar{x}_2)] \tag{4.42}$$

$$b_2 = -\bar{u}\bar{x}_1\bar{x}_2 h_u(\bar{u},\bar{x}_1)\{g_{1x_1}(\bar{x}_1,\bar{u})-q_{1x_1}(\bar{x}_1,\bar{x}_2,\bar{u})\}\{g_{2x_2}(\bar{x}_2)-q_{2x_2}(\bar{x}_1,\bar{x}_2)\}$$

$$- \{\bar{u}h_u(\bar{u},\bar{x}_1)+\bar{x}_2(g_{2x_2}(\bar{x}_2)-q_{2x_2}(\bar{x}_1,\bar{x}_2))\}[\bar{u}\bar{x}_1 h_u(\bar{u},\bar{x}_1)\{g_{1x_1}(\bar{x}_1,\bar{u})$$

$$-q_{1x_1}(\bar{x}_1,\bar{x}_2,\bar{u})\}+\bar{x}_1\bar{x}_2\{(g_{1x_1}(\bar{x}_1,\bar{u})-q_{1x_1}(\bar{x}_1,\bar{x}_2,\bar{u}))(g_{2x_2}(\bar{x}_2)-q_{2x_2}(\bar{x}_1,\bar{x}_2))$$

$$-q_{1x_2}(\bar{x}_1,\bar{x}_2,\bar{u})\cdot q_{2x_1}(\bar{x}_1,\bar{x}_2)\}-\bar{u}\bar{x}_1 h_{x_1}(\bar{u},\bar{x}_1)\{g_{1u}(\bar{x}_1,\bar{u})-q_{1u}(\bar{x}_1,\bar{x}_2,\bar{u})\}]$$

$$+ \bar{u}\bar{x}_1\bar{x}_2[h_u(\bar{u},\bar{x}_1)\{(g_{1x_1}(\bar{x}_1,\bar{u})-q_{1x_1}(\bar{x}_1,\bar{x}_2,\bar{u}))(g_{2x_2}(\bar{x}_2)-q_{2x_2}(\bar{x}_1,\bar{x}_2))$$

$$-q_{1x_2}(\bar{x}_1,\bar{x}_2,\bar{u})\cdot q_{2x_1}(\bar{x}_1,\bar{x}_2)\}-h_{x_1}(\bar{u},\bar{x}_1)\{g_{1u}(\bar{x}_1,\bar{u})-q_{1u}(\bar{x}_1,\bar{x}_2,\bar{u})\}$$

$$\cdot\{g_{2x_2}(\bar{x}_2)-q_{2x_2}(\bar{x}_1,\bar{x}_2)\}] \qquad (4.43)$$

and

$$b_3 = -[\bar{u}h_u(\bar{u},\bar{x}_1)+\bar{x}_2\{g_{2x_2}(\bar{x}_2)-q_{2x_2}(\bar{x}_1,\bar{x}_2)\}]\cdot[\bar{u}\bar{x}_2 h_u(\bar{u},\bar{x}_1)\{g_{2x_2}(\bar{x}_2)$$

$$-q_{2x_2}(\bar{x}_1,\bar{x}_2)\}] \qquad (4.44)$$

We shall now prove the following Hopf-Bifurcation Theorem.

Theorem 4.8. Let $(\bar{u},\bar{x}_1,\bar{x}_2)$ be an interior equilibrium state of the system (4.1), lying in the positive octant of the phase space of the variables u,x_1,x_2. Also, let the following conditions hold

(i) $a_1 > 0$, $a_2 > 0$, $a_3 > 0$,

(ii) $\exists\alpha_0 > 0$ such that $b_1\alpha_0^2 + b_2\alpha_0 + b_3 = 0$ and $b_2^2 > 4b_1b_3$

where a_1,a_2,a_3,b_1,b_2,b_3 are given by (4.40), (4.42), (4.43) and (4.44) respectively. Then, as the value of α (the bifurcation

parameter) passes through α_0, there appear small amplitude periodic solutions of the system (4.1), bifurcating from the equilibrium state $(\bar{u},\bar{x}_1,\bar{x}_2)$.

Proof: First we observe that at $\alpha = \alpha_0$, the characteristic equation has one real and a pair of imaginary roots because at $\alpha = \alpha_0$, $a_1 > 0$, $a_2 > 0$, $a_3 > 0$ from (i) and

$$(a_1a_2-a_3)_{\alpha=\alpha_0} = b_1\alpha_0^2 + b_2\alpha_0 + b_3 = 0 \quad \text{from (ii) and (4.41).}$$

Next we shall show that the eigenvalues cross the imaginary axis with non-zero speed at $\alpha = \alpha_0$. To do this, let us assume that for values of α near α_0, the eigenvalues are of the form

$$\lambda_1 \pm i\lambda_2, \quad \lambda_3$$

where $\lambda_1,\lambda_2,\lambda_3$ are real numbers. In view of this, the characteristic equation will look like

$$\lambda^3 - (\lambda_3+2\lambda_1)\lambda^2 + (\lambda_1^2+\lambda_2^2+2\lambda_1\lambda_3)\lambda - (\lambda_1^2+\lambda_2^2)\lambda_3 = 0 \tag{4.45}$$

Now comparing equations (4.40) and (4.45), we get

$$\left.\begin{aligned} a_1 &= -(\lambda_3+2\lambda_1) \\ a_2 &= \lambda_1^2 + \lambda_2^2 + 2\lambda_1\lambda_3 \\ a_3 &= -(\lambda_1^2 + \lambda_2^2)\lambda_3 \end{aligned}\right\} \tag{4.46}$$

From these, eliminating λ_2,λ_3, we get the following equation in λ_1

$$(a_1 a_2 - a_3) + 2\lambda_1 \{a_2 + (a_1 + 2\lambda_1)^2\} = 0 \tag{4.47}$$

Since we want to know how λ_1 varies with respect to the parameter α, we differentiate relation (4.47) with respect to

$$\frac{d}{d\alpha}(a_1 a_2 - a_3) + 2\frac{d\lambda_1}{d\alpha}\{a_2 + (a_1 + 2\lambda_1)^2\}$$

$$+ 2\lambda_1 \left\{ \frac{da_2}{d\alpha} + 2(a_1 + 2\lambda)\left(\frac{da_1}{d\alpha} + 2\frac{d\lambda_1}{d\alpha}\right) \right\} = 0$$

We know that at $\alpha = \alpha_0$, $(\lambda_1)_{\alpha=\alpha_0} = 0$, hence

$$(2b_1\alpha_0 + b_2) + 2\left(\frac{d\lambda_1}{d\alpha}\right)_{\alpha=\alpha_0} \{a_2 + a_1^2\}_{\alpha=\alpha_0} = 0$$

or $$\left(\frac{d\lambda_1}{d\alpha}\right)_{\alpha=\alpha_0} = -\frac{2b_1\alpha_0 + b_2}{2(a_1^2 + a_2)_{\alpha=\alpha_0}} = \pm \frac{\sqrt{b_2^2 - 4b_1 b_3}}{2(a_1^2 + a_2)_{\alpha=\alpha_0}} \neq 0.$$

This shows that as α passes through α_0, the eigenvalues corss the imaginary axis transversally, i.e. with non-zero speed.

Also, from (4.46) we observe that

$$(\lambda_3)_{\alpha=\alpha_0} = -a_1 < 0.$$

Now application of the Hopf-bifurcation theorem, mentioned in Chapter II, proves the theorem.

Note: Critical value α_0 of the bifurcation parameter α is a root of the following quadratic equation

$$b_1\alpha^2 + b_2\alpha + b_3 = 0$$

where b_1, b_2, b_3 are given by (4.42), (4.43), (4.44) respectively. If $b_1 = 0$, then we have a unique α_0 i.e.

$$\alpha_0 = -\frac{b_3}{b_2},$$

in which case we will require $b_2 \cdot b_3 < 0$ to get a feasible bifurcation value. But if $b_1 \neq 0$, then depending upon the relative magnitudes and signs of b_1, b_2, b_3, we will have one, two or none of such values. In general

$$\alpha_0 = \frac{-b_2 \pm \sqrt{b_2^2 - 4b_1 b_3}}{2b_1} \tag{4.47}$$

Since α is taken to be positive, only positive roots in (4.47) are admissible.

4.8. A Special Case.

Here we consider a specific model, which incorporates a cost associated with the help to the mutualist by the mutualist-competitor. The model considered in the Section 6 does not have this feature. This would be applicable to those biological systems in which the growth rate of the mutualist-competitor is hindered by the presence of the mutualist, when the other competitor is not around. Help to the mutualist-competitor by the mutualist comes only if there is another species which competes with the mutualist-competitor. We consider the

the following model

$$\left.\begin{aligned} u' &= \gamma u\left(1 - \frac{u}{L} + \theta x_1\right) \\ x_1' &= \alpha x_1\left(1 - \frac{x_1}{K_1} - \frac{\xi u}{a+x_1}\right) - \frac{\alpha\beta x_1 x_2}{1+mu} \\ x_2' &= \delta x_2\left(1 - \frac{x_2}{K_2}\right) - \eta x_1 x_2 \end{aligned}\right\} \tag{4.48}$$

where parameters $\alpha,\beta,\gamma,\delta,\eta,a,\theta,m,\xi,L,K_1,K_2$ are all positive.

In this section, we shall find specific conditions, in terms of the above parameters, for the existence of periodic solutions of the system (4.48), using our Theorem 4.8. For this we would be interested in interior equilibria only.

The interior equilibrium, if it exists, is obtained by solving the equations

$$1 - \frac{u}{L} + \theta x_1 = 0$$

$$1 - \frac{x_1}{K_1} - \frac{\xi u}{a+x_1} - \frac{\beta x_2}{1+mu} = 0$$

$$\delta\left(1 - \frac{x_2}{K_2}\right) - \eta x_1 = 0.$$

By eliminating u,x_2 the equation for x_1 appears in the form

$$\begin{aligned} &\delta mL\theta x_1^3 - \{\beta\eta K_1K_2 + \delta K_1 mL\theta - \delta(1+mL) - a\delta mL\theta - \delta\xi K_1 mL^2\theta^2\}x_1^2 \\ &+ \{(1+mL)(a\delta + \delta\xi LK_1\theta - K_1) + \delta\xi K_1 mL^2\theta + \delta\beta K_1K_2 - a\delta K_1 mL\theta - a\beta\eta K_1K_2\}x_1 \\ &- \delta K_1\{(a-\xi L)(1+mL) - a\beta K_2\} = 0. \end{aligned} \tag{4.49}$$

Thus we can expect up to three equilibrium states in the interior to the positive octant. The existence of any such equilibria depends upon the relative magnitudes of all the parameters.

Now let us assume that there exists at least one interior equilibrium $E^*(\bar{u},\bar{x}_1,\bar{x}_2)$, where $\bar{x}_1$ satisfies the equation (4.49). and $\bar{u}$, $\bar{x}_2$ are given by

$$\left.\begin{aligned} \bar{u} &= L(1+\theta\bar{x}_1) \\ \bar{x}_2 &= \frac{K_2}{\delta}(\delta-\eta\bar{x}_1). \end{aligned}\right\} \tag{4.50}$$

We further assume that $\bar{x}_1 < \dfrac{\delta}{\eta}$, (4.51)

so that $\bar{x}_2 > 0$.

Comparing model (4.48) with the general model we find that in the present case

$$\left.\begin{aligned} h(u,x_1) &= \gamma(1-\frac{u}{L}+\theta x_1) \\ g_1(x_1,u) &= 1-\frac{x_1}{K_1}-\frac{\xi u}{a+x_1} \\ g_2(x_2) &= \delta(1-\frac{x_2}{K_2}) \\ q_1(x_1,x_2,u) &= \frac{\beta x_2}{1+mu} \\ q_2(x_1,x_2) &= \eta x_1. \end{aligned}\right\} \tag{4.52}$$

Now we find various partial derivatives, required to compute the stability conditions.

$$\left.\begin{aligned}
&h_u(u,x_1) = -\frac{\gamma}{L}, \quad h_{x_1}(u,x_1) = \gamma\theta \\
&g_{1u}(x_1,u) = -\frac{\xi}{a+x_1}, \quad g_{1x_1} = \frac{\xi u}{(a+x_1)^2} - \frac{1}{K_1}, \quad g_{2x_2}(x_2) = -\frac{\delta}{K_2} \\
&q_{1u}(x_1,x_2,u) = \frac{-\beta m x_2}{(1+mu)^2}, \quad q_{1x_1} = 0, \quad q_{1x_2} = \frac{\beta}{1+mu} \\
&q_{2x_1}(x_2) = \eta, \quad q_{2x_2}(x_2) = 0.
\end{aligned}\right\} \tag{4.53}$$

The characteristic equation at $(\bar{u},\bar{x}_1,\bar{x}_2)$, then can be obtained by using equation (4.40). It is given by

$$\lambda^3 + a_1\lambda^2 + a_2\lambda + a_3 = 0 \tag{4.54}$$

where a_1,a_2,a_3 are to be computed from (4.40), (4.50) and (4.53). We can show that a_1,a_2,a_3 assume the following form in this case

$$a_1 = \frac{\gamma\bar{u}}{L} + \frac{\delta\bar{x}_2}{K_2} - \alpha\bar{x}_1\left(\frac{\xi\bar{u}}{(a+\bar{x}_1)^2} - \frac{1}{K_1}\right) \tag{4.55}$$

$$\begin{aligned} a_2 = {} & \frac{\gamma\bar{u}}{L}\left\{\frac{\delta\bar{x}_2}{K_2} - \alpha\bar{x}_1\left(\frac{\xi\bar{u}}{(a+\bar{x}_1)^2} - \frac{1}{K_1}\right)\right\} - \alpha\bar{x}_1\bar{x}_2\left\{\frac{\delta}{K_2}\left(\frac{\xi\bar{u}}{(a+\bar{x}_1)^2} - \frac{1}{K_1}\right)\right. \\ & \left. + \frac{\beta\eta}{1+m\bar{u}}\right\} + \alpha\gamma\theta\bar{u}\bar{x}_1\left\{\frac{\xi}{a+\bar{x}_1} - \frac{\beta m\bar{x}_2}{(1+m\bar{u})^2}\right\} \end{aligned} \tag{4.56}$$

$$a_3 = \alpha\gamma\bar{u}\bar{x}_1\bar{x}_2\left[\frac{\delta\theta}{K_2}\left\{\frac{\xi}{a+\bar{x}_1} - \frac{\beta m\bar{x}_2}{(1+m\bar{u})^2}\right\} - \frac{1}{L}\left\{\left(\frac{\xi\bar{u}}{(a+\bar{x}_1)^2} - \frac{1}{K_1}\right)\frac{\delta}{K_2} + \frac{\beta\eta}{1+m\bar{u}}\right\}\right] \tag{4.57}$$

Next we calculate $(a_1a_2-a_3)$. Written as a function of the parameter

α, it becomes

$$a_1a_2 - a_3 = b_1\alpha^2 + b_2\alpha + b_3 \tag{4.58}$$

where we can show that

$$b_1 = \left(\frac{\xi\bar{u}}{(a+\bar{x}_1)^2} - \frac{1}{K_1}\right)\bar{x}_1^2\left[\frac{\gamma\bar{u}}{L}\left(\frac{\xi\bar{u}}{(a+\bar{x}_1)^2} - \frac{1}{K_1}\right) - \gamma\theta\bar{u}\left(\frac{\xi}{a+\bar{x}_1} - \frac{\beta m\bar{x}_2}{(1+m\bar{u})^2}\right)\right.$$
$$\left. + \bar{x}_2\left\{\frac{\delta}{K_2}\left(\frac{\xi\bar{u}}{(a+\bar{x}_1)^2} - \frac{1}{K_1}\right) + \frac{\beta\eta}{1+m\bar{u}}\right\}\right] \tag{4.58}$$

$$b_2 = -\frac{\gamma\delta\bar{u}\bar{x}_1\bar{x}_2}{LK_2}\left(\frac{\xi\bar{u}}{(a+\bar{x}_1)^2} - \frac{1}{K_1}\right) - \left(\frac{\gamma\bar{u}}{L} + \frac{\delta\bar{x}_2}{K_2}\right)\frac{\gamma\bar{u}\bar{x}_1}{L}\left(\frac{\xi\bar{u}}{(a+\bar{x}_1)^2} - \frac{1}{K_1}\right)$$
$$- \frac{\delta\bar{x}_1\bar{x}_2^2}{K_2}\left\{\left(\frac{\xi\bar{u}}{(a+\bar{x}_1)^2} - \frac{1}{K_1}\right)\frac{\delta}{K_2} + \frac{\beta\eta}{1+m\bar{u}}\right\}$$
$$+ \frac{\theta\gamma^2\bar{u}^2\bar{x}_1^2}{L}\left\{\frac{\xi}{a+\bar{x}_1} - \frac{\beta m\bar{x}_2}{(1+m\bar{u})^2}\right\} \tag{4.59}$$

and

$$b_3 = \frac{\gamma\delta\bar{u}\bar{x}_2}{LK_2}\left(\frac{\gamma\bar{u}}{L} + \frac{\delta\bar{x}_2}{K_2}\right). \tag{4.60}$$

Since $b_3 > 0$, we can find α_0 which satisfies the condition (ii) of the Theorem 4.8, if any one of the following holds

1. $b_1 \geq 0, \quad b_2 < 0$
2. $b_2 \geq 0, \quad b_1 < 0$
3. $b_1 < 0, \quad b_2 < 0.$

The following result is a Corollary to Theorem 4.8.

Corollary 4.9. Let a_1, a_3, b_1, b_2, b_3 be as given by (4.55), (4.57)-(4.60). If $a_1, a_3 > 0$ and $\exists\, \alpha_0 \ni b_1\alpha_0^2 + b_2\alpha_0 + b_3 = 0$ and $2b_1\alpha_0 + b_2 \neq 0$, then the parameter α acts as a bifurcation parameter in the sense that when α takes its values through α_0, the equilibrium E^* bifurcates into periodic orbits at $\alpha = \alpha_0$.

We now give numerical examples to illustrate the validity and practical realization of our Theorem 4.8. Consider

Example 1.

$$\left.\begin{aligned} u' &= \frac{u}{10}(1-u+x_1) \\ x_1' &= \alpha x_1\left(1-x_1 - \frac{572}{1155}\cdot\frac{u}{(1+x_1)}\right) - \frac{\alpha x_1 x_2}{1+u} \\ x_2' &= x_2(1-x_2) - \frac{3x_1x_2}{2} \end{aligned}\right\} \tag{4.61}$$

We find that $\bar{u} = \frac{11}{10}$, $\bar{x}_1 = \frac{1}{10}$, $\bar{x}_2 = \frac{17}{20}$ is an equilibrium state. Calculations at $E^*(\frac{11}{10}, \frac{1}{10}, \frac{17}{20})$ show that

$$a_1 = .0096 + .0549\alpha > 0$$

$$a_3 = .0008\alpha > 0$$

$$b_1 = -.0002, \quad b_2 = -.0006, \quad b_3 = .0897$$

and the bifurcation value of the parameter α comes out to be approximately 19.73.

Example 2. We construct this example by using perturbation techniques. First we find conditions which guarantee the existence of a periodic

orbit in the $u-x_1$ plane. Then we introduce the species x_2 and choose parameters in such a way that even a little above the ux_1 plane, growth rates of species u,x_1,x_2 remain close to zero and the periodic orbits of the plane now become three dimensional periodic orbits.

In two dimensions system (4.48) becomes

$$\begin{aligned} u' &= \gamma u\left(1 - \frac{u}{L} + \theta x_1\right) \\ x_1' &= \alpha x_1\left(1 - \frac{x_1}{K_1} - \frac{\xi u}{a+x_1}\right) \end{aligned} \tag{4.62}$$

It can be shown that for $K_1 = 10$, $\theta = 1$, $a = 3$, $L = 3$ and $\xi = \frac{3}{5}$, $E^*(\bar{u},\bar{x}_1)$ where $\bar{u} = 6$, $\bar{x}_1 = 1$, is an equilibrium state for (4.62) and further that we get periodic orbits (Hopf-bifurcation) whenever $\alpha = 16\gamma > 0$.

We now consider the three dimensional model (4.48) and choose the remaining parameters as

$$K_2 = 1, \quad \delta = 0.2739, \quad \eta = 0.2639, \quad m = 1 \quad \text{and} \quad \beta = .01.$$

We can show that at $\bar{u} = 6$, $\bar{x}_1 = 1$, $\bar{x}_2 = 0.0365$, growth rates of species u,x_1,x_2 are $0(10^{-5})$. Hence correct up to four decimal places $E^*(6,1,.0365)$ is an equilibrium state for (4.48).

Computing a_1,a_2,a_3 and $a_1a_2-a_3$ we find that for $\gamma = 1$

$$a_1 = 2.0099 - 0.125\alpha$$

$$a_2 = 0.0198 + 0.6488\alpha$$

$$a_3 = .0064\alpha$$

$$a_1a_2-a_3 = .0811\alpha^2 - 1.3128\alpha + .0397$$

so that there are two values of α, i.e. .0308 and 16.1565 at which $a_1a_2-a_3 = 0$ and $a_1 > 0$, $a_3 > 0$. Thus all the hypotheses of the Theorem 4.8 are satisfied and we shall have perturbed periodic solutions in three dimensions.

4.9. Summary.

In this chapter, a competitor-competitor-mutualist system has been modelled and analyzed. Conditions for the existence of equilibria were given, and the stability of these equilibria determined. As well, conditions for the existence of periodic solutions have been determined.

The discussion of Section 4.6 shows that the mutualist will play a very important role in an ecosystem modelled by model (4.12). For example in Cases A and C, in which the inhibitory effect of the species x_2 on the species x_1 is high (i.e. β large), the mutualist reduces the effectiveness of the competition coefficient β and thereby could cause the reversal of stability of the equilibrium state E_6 in both the cases and reverse competitive outcome, provided the parameter m is sufficiently large. Also, we know that in the absence of the mutualist, the competitive subcommunity of our model (4.12) does not admit any interior equilibrium in Case C, but the introduction of a mutualist into the system always gaurantees an equilibrium state. This shows that the mutualist could change competitive exclusion to coexistence.

In Case D, where nonequilibrium conditions hold, the effect of the mutualist is to cause the competitor x_2 to go to extinction.

In this case, the mutualist u and the competitor x_1 approach equilibrium conditions.

In Section 4.8, by considering a model, which incorporates a cost to the mutualist-competitor of providing direct benefits to the mutualist (model of Section 4.6 does not have this feature), we have established the possibility for the existence of periodic fluctuations in populations of the community. Here, by assigning relative numerical values to the parameters of the system, we have demonstrated the feasibility of such oscillations.

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APPENDIX

In this appendix we shall perform the stability analysis of the periodic orbits, guaranteed by Theorem 3.9 of Chapter III, using the centre manifold theory. We rewrite the system (3.39)

$$\left.\begin{aligned} u' &= \gamma u\left(1 - \frac{u}{L_0+\ell x}\right) \\ x' &= \alpha x\left(1 - \frac{x}{K}\right) - \frac{\beta xy}{1+mu} \\ y' &= y\left(-s + \frac{c\beta x}{1+mu}\right) \end{aligned}\right\} \tag{1}$$

Then we make a change of variables given by

$$\left.\begin{aligned} u - u^* &= u_1 \\ x - x^* &= x_1 \\ y - y^* &= y_1 \end{aligned}\right\} \tag{2}$$

where (u^*,x^*,y^*) is the interior equilibrium state for the system (1) and is given by (3.40). In terms of the new variables, system (1) becomes

$$\left.\begin{aligned} u_1' &= -\gamma u_1 + \gamma\ell x_1 + F_1(u_1,x_1,y_1) \\ x_1' &= \frac{ms\alpha}{c\beta}\left(1 - \frac{x^*}{K}\right)u_1 - \frac{\alpha x^*}{K}x_1 - \frac{s}{c}y_1 + F_2(u_1,x_1,y_1) \\ y_1' &= \frac{-ms\alpha}{\beta}\left(1 - \frac{x^*}{K}\right)u_1 + c\alpha\left(1 - \frac{x^*}{K}\right)x_1 + F_3(u_1,x_1,y_1) \end{aligned}\right\} \tag{3}$$

where $F_1(u_1,x_1,y_1)$, $F_2(u_1,x_1,y_1)$ and $F_3(u_1,x_1,y_1)$ are same as given by (3.48)

According to Theorem 3.9, the zero solution of (3), will bifurcate into periodic orbits when the bifurcation parameter α passes through a critical value α_0. For stability analysis of these periodic orbits, the first step is to transform the variational matrix at (0,0,0) to canonical form for $\alpha = \alpha_0$.

I. Canonical Form.

The variational matrix for (3) at (0,0,0) can be written as

$$\left.\begin{aligned}
&A = \begin{bmatrix} p_1 & p_2 & 0 \\ p_3 & p_4 & p_5 \\ p_6 & p_7 & 0 \end{bmatrix}, \quad \alpha = \alpha_0 \\
&\text{where} \\
&p_1 = -\gamma, \quad p_2 = \gamma\ell, \quad p_3 = \frac{ms\alpha_0}{c\beta}\left(1 - \frac{x^*}{K}\right) \\
&p_4 = -\frac{\alpha_0 x^*}{K}, \quad p_5 = -\frac{s}{c}, \quad p_6 = -\frac{ms\alpha_0}{\beta}\left(1 - \frac{x^*}{K}\right) \\
&\text{and} \quad p_7 = c\alpha_0\left(1 - \frac{x^*}{K}\right).
\end{aligned}\right\} \tag{4}$$

We observe the following relations

$$\left.\begin{aligned}
\ell p_1 + p_2 &= 0 \\
cp_3 + p_6 &= 0 \\
\frac{cp_6}{ms} + p_7 &= 0
\end{aligned}\right\} \tag{5}$$

From the relation (3.64), we know that eigenvalues of the matrix A

at $\alpha = \alpha_0$ are given as

$$\left.\begin{aligned} &\lambda_1 = i\sqrt{a_2}\,, \quad \lambda_2 = -i\sqrt{a_2}\,, \quad \lambda_3 = -\left(\gamma + \frac{\alpha_0 x^*}{K}\right) \\ &\text{where} \\ &a_2 = (1 - \frac{s\lambda}{c\beta K})(1 - \frac{\gamma \ell m}{c\beta})\alpha_0 s + \frac{\alpha_0 s\lambda\gamma}{c\beta K} > 0 \end{aligned}\right\} \tag{6}$$

To effect the canonical transformation of the matrix A, we need to find out eigenvectors corresponding to the above eigenvalues. We shall first find an eigenvector corresponding to the real eigenvalue λ_3. If we denote this by the column vector B then

$$AB = \lambda_3 B \tag{7}$$

If $B = [B_1, B_2, B_3]^T$, then from (4) and (7), we get the following equations to determine B_1, B_2, B_3

$$\left.\begin{aligned} (p_1-\lambda_3)B_1 + p_2B_2 &= 0 \\ p_3B_1 + (p_4-\lambda_3)B_2 + p_5B_3 &= 0 \\ p_6B_1 + p_7B_2 - \lambda_3B_3 &= 0. \end{aligned}\right\} \tag{8}$$

The augmented matrix for this system can be written as

$$\left[\begin{array}{ccc|c} p_1-\lambda_3 & p_2 & 0 & 0 \\ p_3 & p_4-\lambda_3 & p_5 & 0 \\ p_6 & p_7 & -\lambda_3 & 0 \end{array}\right]$$

By elementary row operations and making use of relations given in (4), the above matrix reduces to

$$\left[\begin{array}{ccc|c} 1 & \dfrac{p_2}{p_1-\lambda_3} & 0 & 0 \\ 0 & 1 & \dfrac{p_5}{p_4-\lambda_3-\dfrac{p_2p_3}{p_1-\lambda_3}} & 0 \\ 0 & 0 & 0 & 0 \end{array}\right]$$

From this we can get a set of values,

$$B_1 = \frac{p_2p_5}{p_1-\lambda_3}, \quad B_2 = -p_5 \quad \text{and} \quad B_3 = p_4 - \lambda_3 - \frac{p_2p_3}{p_1-\lambda_3}$$

which satisfy the equation (8). Thus

$$B = \begin{bmatrix} \dfrac{p_2p_5}{p_1-\lambda_3} \\ -p_5 \\ p_4 - \lambda_3 - \dfrac{p_2p_3}{p_1-\lambda_3} \end{bmatrix} = \begin{bmatrix} \dfrac{-\gamma s\ell K}{c\alpha_0 x^*} \\ \dfrac{s}{c} \\ \dfrac{\gamma m\ell s}{c\beta x^*}\left[\left(\dfrac{c\beta+\ell ms}{c\beta\ell m}\right)\lambda-K\right] \end{bmatrix} \tag{9}$$

Similarly we can find eigenvectors corresponding to the pair of imaginary eigenvalues in (6). For this we have to deal with the following augmented matrix

$$\left[\begin{array}{ccc|c} p_1 - i\sqrt{a_2} & p_2 & 0 & 0 \\ p_3 & p_4 - i\sqrt{a_2} & p_5 & 0 \\ p_6 & p_7 & -i\sqrt{a_2} & 0 \end{array}\right]$$

We can show that the eigenvectors corresponding to imaginary eigenvalues can be taken as

$$\begin{bmatrix} \dfrac{p_1 p_2 p_5}{p_1^2 + a_2} \\ -p_5 \\ p_4 - \dfrac{p_1 p_2 p_3}{p_1^2 + a_2} \end{bmatrix} \quad \text{and} \quad \begin{bmatrix} \dfrac{p_2 p_5 \sqrt{a_2}}{p_1^2 + a_2} \\ 0 \\ -\sqrt{a_2}\left(1 + \dfrac{p_2 p_3}{p_1^2 + a_2}\right) \end{bmatrix} . \tag{10}$$

Thus the eigenspace of the eigenvalues of the linearization matrix A is spanned by vectors given by (9) and (10). Now we consider the following matrix T, whose columns are the above mentioned eigenvectors

$$T = \begin{bmatrix} \dfrac{p_1 p_2 p_5}{p_1^2 + a_2} & \dfrac{p_2 p_5 \sqrt{a_2}}{p_1^2 + a_2} & \dfrac{p_2 p_5}{p_1 - \lambda_3} \\ -p_5 & 0 & -p_5 \\ p_4 - \dfrac{p_1 p_2 p_3}{p_1^2 + a_2} & -\sqrt{a_2}\left(1 + \dfrac{p_2 p_3}{p_1^2 + a_2}\right) & p_4 - \lambda_3 - \dfrac{p_2 p_3}{p_1 - \lambda_3} \end{bmatrix} . \tag{11}$$

The matrix T has the property that a new set of variables v_1, v_2, v_3 (say) and the old variables u_1, x_1, y_1, connected by the relation

$$\begin{bmatrix} u_1 \\ x_1 \\ y_1 \end{bmatrix} = T \begin{bmatrix} v_1 \\ v_2 \\ v_3 \end{bmatrix} \tag{12}$$

are such that the system (3) transforms to the required canonical form in the variables v_1, v_2, v_3, which are referred to as canonical variables. The matrix of the transformation (i.e.T) is a non-singular matrix, which could be checked by evaluating the determinant of T.

$$\det. T = p_2 p_5^2 \sqrt{a_2} \left[-\frac{p_1}{p_1^2+a_2}\left(1+\frac{p_2p_3}{p_1^2+a_2}\right) + \frac{1}{p_1^2+a_2}\left(p_4-\lambda_3-\frac{p_2p_3}{p_1-\lambda_3}\right)\right.$$

$$\left. + \frac{1}{p_1-\lambda_3}\left(1+\frac{p_2p_3}{p_1^2+a_2}\right) - \frac{1}{p_1^2+a_2}\left(p_4-\frac{p_1p_2p_3}{p_1^2+a_2}\right)\right]$$

$$= p_2 p_5^2 \sqrt{a_2}\left[-\frac{p_1}{p_1^2+a_2} - \frac{\lambda_3}{p_1^2+a_2} + \frac{1}{p_1-\lambda_3}\right]$$

$$= p_2 p_5^2 \sqrt{a_2}\left[\frac{\gamma}{p_1^2+a_2} + \frac{\gamma+\alpha_0\frac{x^*}{K}}{p_1^2+a_2} + \frac{1}{\frac{\alpha_0 x^*}{K}}\right] = Q \quad \text{(say)}$$

$$\neq 0.$$

Thus we can find v_1, v_2, v_3 from (12)

$$\begin{bmatrix} v_1 \\ v_2 \\ v_3 \end{bmatrix} = T^{-1}\begin{bmatrix} u_1 \\ x_1 \\ y_1 \end{bmatrix} \tag{13}$$

Let us express the matrix T in the form

$$T = \begin{bmatrix} q_1 & q_2 & q_3 \\ q_4 & 0 & q_5 \\ q_6 & q_7 & q_8 \end{bmatrix} \tag{14}$$

$$\left.\begin{aligned} \text{where} \quad & q_1 = \frac{p_1p_2p_5}{p_1^2+a_2}, \quad q_2 = \frac{p_2p_5\sqrt{a_2}}{p_1^2+a_2}, \quad q_3 = \frac{p_2p_5}{p_1-\lambda_3}, \\ & q_4 = -p_5 = q_5, \qquad\qquad q_6 = p_4 - \frac{p_1p_2p_3}{p_1^2+a_2}, \\ & q_7 = -\sqrt{a_2}\left(1+\frac{p_2p_3}{p_1^2+a_2}\right), \qquad q_8 = p_4 - \lambda_3 - \frac{p_2p_3}{p_1-\lambda_3} \end{aligned}\right\} \tag{15}$$

In terms of these notations

$$T^{-1} = \frac{1}{Q}\begin{bmatrix} w_1 & w_2 & w_3 \\ w_4 & w_5 & w_6 \\ w_7 & w_8 & w_9 \end{bmatrix}$$

$$\left.\begin{array}{lll} \text{where}\quad Q = \det T, & w_1 = -q_5q_7, & w_2 = -q_2q_8 + q_3q_7 \\ w_3 = q_2q_5, & w_4 = -q_4q_8 + q_5q_6, & w_5 = q_1q_8 - q_3q_6 \\ w_6 = -q_1q_5 + q_3q_4, & w_7 = q_4q_7, & w_8 = -q_1q_7 + q_2q_6 \\ w_9 = -q_2q_4 & & \end{array}\right\} \tag{16}$$

Hence

$$\left.\begin{aligned} v_1 &= \frac{1}{Q}\,[w_1u_1+w_2x_1+w_3y_1] \\ v_2 &= \frac{1}{Q}\,[w_4u_1+w_5x_1+w_6y_1] \\ v_3 &= \frac{1}{Q}\,[w_7u_1+w_8x_1+w_9y_1] \end{aligned}\right\} \tag{17}$$

Differentiating the above equations with respect to t and using the system (3), we get the required canonical form i.e.

$$\left.\begin{aligned} v_1' &= \sqrt{a_2}\,v_2 + G_1(v_1,v_2,v_3) \\ v_2' &= -\sqrt{a_2}\,v_1 + G_2(v_1,v_2,v_3) \\ v_3' &= \lambda_3v_3 + G_3(v_1,v_2,v_3) \end{aligned}\right\} \tag{18}$$

where

$$\begin{aligned} G_1(v_1,v_2,v_3) = \frac{1}{Q}\,[w_1\{-\gamma u_1+\gamma\ell x_1+F_1(u_1,x_1,y_1)\}+w_2\{\frac{ms\alpha}{c\beta}\,(1-\frac{x^*}{K})u_1 \\ -\frac{\alpha x^*}{K_1}\,x_1-\frac{s}{c}\,y_1+F_2(u_1,x_1,y_1)\}+w_3\{-\frac{ms\alpha}{\beta}\,(1-\frac{x^*}{K})u_1 \\ +c\alpha(1-\frac{x^*}{K})x_1+F_3(u_1,x_1,y_1)\}] - \sqrt{a_2}\,v_2. \end{aligned}$$

$$G_2(v_1,v_2,v_3) = \frac{1}{Q}\,[w_4\{-\gamma u_1+\gamma\ell x_1+F_1(u_1,x_1,y_1)\}+w_5\{\frac{ms\alpha}{c\beta}\,(1-\frac{x^*}{K})u_1$$
$$-\frac{\alpha x^*}{K}\,x_1-\frac{s}{c}\,y_1+F_2(u_1,x_1,y_1)\}+w_6\{-\,\frac{ms\alpha}{\beta}\,(1-\frac{x^*}{K})\,u_1$$
$$+c\alpha(1-\frac{x^*}{K})x_1+F_3(u_1,x_1,y_1)\}]\,+\,\sqrt{a_2}\,v_1$$

and

$$G_3(v_1,v_2,v_3) = \frac{1}{Q}\,[w_7\{-\gamma u_1+\gamma\ell x_1+F_1(u_1,x_1,y_1)\}+w_8\{\frac{ms\alpha}{c\beta}\,(1-\frac{x^*}{K})u_1$$
$$-\,\frac{\alpha x^*}{K}\,x_1\,-\,\frac{s}{c}\,y_1+F_2(u_1,x_1,y_1)\}+w_9\{-\,\frac{ms\alpha}{\beta}\,(1-\frac{x^*}{K})u_1$$
$$+\,c\alpha(1-\frac{x^*}{K})x_1+F_3(u_1,x_1,y_1)\}]\,-\,\lambda_3 v_3$$

We can show by expanding these expressions that $G_1(v_1,v_2,v_3)$, $G_2(v_1,v_2,v_3)$ and $G_3(v_1,v_2,v_3)$ do not contain any linear term in v_1,v_2,v_3.

II. Centre Manifold.

If

$$v_3 = \phi(v_1,v_2;\alpha_0)$$

is the centre manifold then ϕ contains quadratic and higher order terms only in v_1,v_2. So let us take

$$v_3 = b_1v_1^2 + b_2v_1v_2 + b_3v_2^2 + \text{H.O.T.} \qquad (19)$$

where H.O.T. denotes higher order terms, starting with a polynomial in v_1,v_2,v_3 of degree three, and b_1,b_2,b_3 are the constants to be determined in terms of parameters of our system. From (19)

$$v_3' = (2b_1v_1+b_2v_2)v_1' + (b_2v_1+2b_3v_2)v_2' + \frac{d}{dt}(\text{H.O.T.})$$

$$= (2b_1v_1+b_2v_2)\sqrt{a_2}\, v_2 + (b_2v_1+2b_3v_2)(-\sqrt{a_2}\, v_1) + \text{H.O.T.}$$

$$= -b_2\sqrt{a_2}\, v_1^2 + 2\sqrt{a_2}\,(b_1-b_3)v_1v_2 + b_2\sqrt{a_2}\, v_2^2 + \text{H.O.T.} \tag{20}$$

and from (18)

$$v_3' = \lambda_3 v_3 + G_3(v_1,v_2,v_3). \tag{21}$$

We are interested in the second order terms in v_1, v_2, so that we need to consider G_3 and use the relations

$$u_1 = q_1v_1 + q_2v_2 + q_3v_3$$

$$x_1 = q_4v_1 + q_5v_3$$

$$y_1 = q_6v_1 + q_7v_2 + q_8v_3 .$$

We list here only those terms in (21), which will contribute second order terms

$$\begin{aligned} v_3' = {} & \frac{w_7}{Q}\{-\gamma q_3+\gamma\ell q_5\}v_3 - \frac{\gamma}{u^*}\frac{w_7}{Q}\{(\ell^2q_4^2+q_1^2-2\ell q_1q_4)v_1^2 \\ & + (2q_1q_2-2\ell q_2q_4)v_1v_2+q_2^2v_2^2\} + \frac{w_8}{Q}\{\frac{ms\alpha_0}{c\beta}(1-\frac{x^*}{K})q_3 \\ & - \alpha_0\frac{x^*}{K}q_5 - \frac{s}{c}q_8\}v_3 + \frac{w_8}{Q}\cdot\frac{1}{c\beta K(1+mu^*)}\cdot[\{msK\beta q_1q_6-\alpha_0 sm^2(K-x^*)q_1^2 \\ & - cK\beta^2q_4q_6-m\alpha_0\beta c(K-x^*)q_1q_4-(1+mu^*)q_4^2\}v_1^2 \\ & +\{msK\beta(q_1q_7+q_2q_6)-\alpha_0 sm^2(K-x^*)2q_1q_2-cK\beta^2q_4q_7 \\ & -m\alpha_0\beta c(K-x^*)q_2q_4\}v_1v_2+\{msK\beta q_2q_7-\alpha_0 sm^2(K-x^*)q_2^2\}v_2^2] \\ & + \frac{w_9}{Q}\{-\frac{ms\alpha_0}{\beta}(1-\frac{x^*}{K})q_3+c\alpha_0(1-\frac{x^*}{K})q_5\}v_3 + \end{aligned}$$

$$+ \frac{w_9}{Q} \frac{1}{\beta K(1+mu^*)} [\{\alpha_0 sm^2(K-x^*)q_1^2 - m\alpha_0\beta c(K-x^*)q_1q_4 + cK\beta^2 q_4q_6 - ms\beta Kq_1q_6\}v_1^2$$

$$+\{\alpha_0 sm^2(K-x^*)2q_1q_2 - m\alpha_0\beta c(K-x^*)q_2q_4 + cK\beta^2 q_4q_7 - ms\beta K(q_1q_7+q_2q_6)\}v_1v_2$$

$$+\{\alpha_0 sm^2(K-x^*)q_2^2 - ms\beta Kq_2q_7\}v_2^2] + \text{H.O.T.} \tag{22}$$

In this equation v_3 has to be replaced by (19) and then we can compare this with the equation (20) to get three equations to determine b_1, b_2, b_3. Doing this we get the following system of equations

$$\begin{aligned} m_1b_1 + m_2b_2 + 0\,b_3 &= n_1 \\ m_3b_1 + m_4b_2 + m_5b_3 &= n_2 \\ 0\,b_1 + m_6b_2 + m_7b_3 &= n_3 \end{aligned} \tag{23}$$

where

$$m_1 = \frac{w_7}{Q}\{-\gamma q_3 + \gamma \ell q_5\} + \frac{w_8}{Q}\{\frac{ms\alpha_0}{c\beta}(1 - \frac{x^*}{K})q_3 - \alpha_0 \frac{x^*}{K} q_5 - \frac{s}{c} q_8\}$$
$$+ \frac{w_9}{Q}\{-\frac{ms\alpha_0}{\beta}(1 - \frac{x^*}{K})q_3 + c\alpha_0(1 - \frac{x^*}{K})q_5\}$$

$$m_2 = \sqrt{a_2}$$

$$m_3 = -2\sqrt{a_2}$$

$$m_4 = \frac{w_7}{Q}\{-\gamma q_3 + \gamma \ell q_5\} + \frac{w_8}{Q}\{\frac{ms\alpha_0}{c\beta}(1 - \frac{x^*}{K})q_3 - \alpha_0 \frac{x^*}{K} q_5 - \frac{s}{c} q_8\}$$
$$+ \frac{w_9}{Q}\{-\frac{ms\alpha_0}{\beta}(1 - \frac{x^*}{K})q_3 + c\alpha_0(1 - \frac{x^*}{K})q_5\} = m_1$$

$$m_5 = m_4 + 2\sqrt{a_2}$$

$$m_6 = -\sqrt{a_2}$$

$$m_7 = m_4$$

$$-n_1 = -\frac{\gamma w_7}{u^*Q}\{\ell^2 q_4^2 + q_1^2 - 2\ell q_1 q_4\} + \frac{w_8}{Qc\beta K(1+mu^*)}\{msK\beta q_1 q_6 - \alpha_0 sm^2(K-x^*)q_1^2$$

$$-cK\beta^2 q_4 q_6 - m\alpha_0\beta c(K-x^*)q_1 q_4 - (1+mu^*)q_4^2\} + \frac{w_9}{Q\beta K(1+mu^*)}\{\alpha_0 sm^2(K-x^*)q_1^2$$

$$-m\alpha_0\beta c(K-x^*)q_1 q_4 + cK\beta^2 q_4 \cdot q_6 - ms\beta K q_1 q_6\}$$

$$-n_2 = -\frac{\gamma w_7}{u^*Q}\{2q_1 q_2 - 2\ell q_2 q_4\} + \frac{w_8}{Qc\beta K(1+mu^*)}\{msK\beta(q_1 q_7 + q_2 q_6)$$

$$-\alpha_0 sm^2(K-x^*)2q_1 q_2 - cK\beta^2 q_4 q_7 - m\alpha_0\beta c(K-x^*)q_2 q_4\}$$

$$+\frac{w_9}{Q\beta K(1+mu^*)}\{\alpha_0 sm^2(K-x^*)2q_1 q_2 - m\alpha_0\beta c(K-x^*)q_2 q_4$$

$$+cK\beta^2 q_4 q_7 - ms\beta K(q_1 q_7 + q_2 q_6)\}$$

and finally

$$-n_3 = -\frac{\gamma w_7}{u^*Q}q_2^2 + \frac{w_8}{Qc\beta K(1+mu^*)}\{msK\beta q_2 q_7 - \alpha_0 sm^2(K-x^*)q_2^2\}$$

$$+\frac{w_9}{Q\beta K(1+mu^*)}\{\alpha_0 sm^2(K-x^*)q_2^2 - ms\beta K q_2 q_7\}.$$

We have to solve (23) for b_1, b_2, b_3. For this let us assume that

$$D \equiv \det.\begin{bmatrix} m_1 & m_2 & 0 \\ m_3 & m_4 & m_5 \\ 0 & m_6 & m_7 \end{bmatrix} \neq 0 \tag{24}$$

Then using Cramer's rule

$$b_1 = \frac{1}{D}\det\begin{bmatrix} n_1 & m_2 & 0 \\ n_2 & m_4 & m_5 \\ n_3 & m_6 & m_7 \end{bmatrix}$$

$$\left.\begin{aligned}
b_2 &= \frac{1}{D}\det\begin{bmatrix} m_1 & n_1 & 0 \\ m_3 & n_2 & m_5 \\ 0 & n_3 & m_7 \end{bmatrix} \\
\text{and} \\
b_3 &= \frac{1}{D}\det\begin{bmatrix} m_1 & m_2 & n_1 \\ m_3 & m_4 & n_2 \\ 0 & m_6 & n_3 \end{bmatrix}
\end{aligned}\right\} \tag{25}$$

where $m_1,m_2,m_3,m_4,m_5,m_6,m_7,n_1,n_2,n_3$ and D are as given in (23) and (24).

Thus the centre manifold is known i.e.

$$v_3 = h(v_1,v_2) = b_1v_1^2 + b_2v_1v_2 + b_3v_2^2 + \text{H.O.T.} \tag{26}$$

where b_1,b_2,b_3 are given by (25).

III. The flow on the centre manifold is governed by the 2-dimensional system

$$\begin{aligned}
v_1' &= \sqrt{a_2}\; v_2 + G_1(v_1,v_2,h(v_1,v_2)) \\
v_2' &= -\sqrt{a_2}\; v_1 + G_2(v_1,v_2,h(v_1,v_2)).
\end{aligned} \tag{27}$$

According to the centre manifold theory, the system (27) contains all the necessary information needed to determine the asymptotic behaviour of the small amplitude periodic solutions of (18).

Marsden and McCraken have given an explicit formula, to determine the stability behaviour of the periodic orbits. The formula involves various partial derivatives of the functions G_1 and G_2, evaluated

at $v_1 = 0$, $v_2 = 0$.

Just to avoid confusion let us replace

$$G_1 \to G^{(1)}$$

$$G_2 \to G^{(2)}.$$

Then if $\Gamma > 0$, the periodic orbits occur for $\alpha < \alpha_0$ and are unstable, and if $\Gamma < 0$, the periodic orbits occur for $\alpha > \alpha_0$ and are stable, where

$$\Gamma = \frac{3\pi}{4|\lambda(\alpha_0)|}\{G^{(1)}_{111} + G^{(1)}_{122} + G^{(2)}_{112} + G^{(2)}_{222}\}$$

$$+ \frac{3\pi}{4|\lambda(0)|^2}\{-G^{(1)}_{11}\cdot G^{(1)}_{12} + G^{(2)}_{22}\cdot G^{(2)}_{12} + G^{(2)}_{11}\cdot G^{(2)}_{12}$$

$$-G^{(1)}_{22}\cdot G^{(1)}_{12} + G^{(1)}_{11}\cdot G^{(2)}_{11} - G^{(1)}_{22}\cdot G^{(2)}_{22}\} \qquad (28)$$

Here $G^{J}_{i_1 \ldots i_r}$ denote $\frac{\partial^r G^{(J)}}{\partial v_{i_1} \ldots \partial v_{i_r}}$, evaluated at $v_1 = 0 = v_2$.

Now we observe

$$u_1 = q_1v_1 + q_2v_2 + q_3(b_1v_1^2+b_2v_1v_2+b_3v_2^2)$$

$$x_1 = q_4v_1 + q_5(b_1v_1^2+b_2v_1v_2+b_3v_2^2)$$

$$y_1 = q_6v_1 + q_7v_2 + q_8(b_1v_1^2+b_2v_1v_2+b_3v_2^2)$$

Since we are concerned only with 2nd and 3rd order terms, we collect such terms in $G^{(1)}$ and $G^{(2)}$. Let $M(v_1,v_2)$ denote such terms in $G^{(1)}$ and $N(v_1,v_2)$ in $G^{(2)}$. Then

$$M(v_1,v_2) = \left[\frac{w_1}{Q}(-\gamma q_3+\gamma\ell q_5) + \frac{w_2}{Q}\left\{\frac{ms\alpha_0}{c\beta}(1-\frac{x^*}{K})q_3 - \frac{\alpha_0 x^*}{K}q_5 - \frac{s}{c}q_8\right\}\right.$$
$$\left. + \frac{w_3}{Q}\left\{\frac{-ms\alpha_0}{\beta}(1-\frac{x^*}{K})q_3 + c\alpha_0(1-\frac{x^*}{K})q_5\right\}\right](b_1v_1^2+b_2v_1v_2+b_3v_2^2)$$
$$+ \frac{1}{Q}[w_1F_1(u_1,x_1,y_1)+w_2F_2(u_1,x_1,y_1)+w_3F_3(u_1,x_1,y_1)]$$

and similarly

$$N(v_1,v_2) = \frac{1}{Q}\left[w_4(-\gamma q_3+\gamma\ell q_5)+w_5\left\{\frac{ms\alpha_0}{c\beta}(1-\frac{x^*}{K})q_3 - \frac{\alpha_0 x^*}{K}q_5 - \frac{s}{c}q_8\right\}\right.$$
$$\left. + w_6\left\{-\frac{ms\alpha_0}{\beta}(1-\frac{x^*}{K})q_3+c\alpha_0(1-\frac{x^*}{K})q_5\right\}\right](b_1v_1^2+b_2v_1v_2+b_3v_2^2)$$
$$+ \frac{1}{Q}[w_4F_1(u_1,x_1,y_1)+w_5F_2(u_1,x_1,y_1)+w_6F_3(u_1,x_1,y_1)].$$

If we denote

$$L_1 \equiv \frac{1}{Q}\left[w_1(-\gamma q_3+\gamma\ell q_5)+w_5\left\{\frac{ms\alpha_0}{c\beta}(1-\frac{x^*}{K})q_3 - \frac{\alpha_0 x^*}{K}q_5 - \frac{s}{c}q_8\right\}\right.$$
$$\left. +w_3\left\{-\frac{ms\alpha_0}{\beta}(1-\frac{x^*}{K})q_3+c\alpha_0(1-\frac{x^*}{K})q_5\right\}\right] \tag{29}$$

and

$$L_2 \equiv \frac{1}{Q}\left[w_4(-\gamma q_3+\gamma\ell q_5)+w_5\left\{\frac{ms\alpha_0}{c\beta}(1-\frac{x^*}{K})q_3 - \frac{\alpha_0 x^*}{K}q_5 - \frac{s}{c}q_8\right\}\right.$$
$$\left. +w_6\left\{-\frac{ms\alpha_0}{\beta}(1-\frac{x^*}{K})q_3+c\alpha_0(1-\frac{x^*}{K})q_5\right\}\right] \tag{30}$$

then

$$M(v_1,v_2) = L_1(b_1v_1^2+b_2v_1v_2+b_3v_2^2) + \frac{1}{Q}[w_1F_1+w_2F_2+w_3F_3] \tag{31}$$

$$N(v_1,v_2) = L_2(b_1v_1^2+b_2v_1v_2+b_3v_2^2) + \frac{1}{Q}[w_4F_1+w_5F_2+w_6F_3] \qquad (32)$$

Now using (3.48), we need to know F_1, F_2, F_3 as a function of v_1, v_2.

$$F_1 = -\frac{\gamma}{u^*}[\ell x_1-u_1]^2\left(1+\frac{\ell x_1}{u^*}\right)^{-1}$$

$$= -\frac{\gamma}{u^*}[\ell x_1-u_1]^2\left(1-\frac{\ell x_1}{u^*}\right) + \text{H.O.T.}$$

$$= -\frac{\gamma}{u^*}[(\ell q_4-q_1)v_1-q_2v_2+(\ell q_5-q_3)(b_1v_1^2+b_2v_1v_2+b_3v_2^2)]^2[1-$$

$$\frac{\ell}{u^*}\{q_4v_1+q_5(b_1v_1^2+b_2v_1v_2+b_3v_2^2)\}]$$

$$= -\frac{\gamma}{u^*}[(\ell^2q_4^2+q_1^2-2\ell q_1q_4)v_1^2+(2q_1q_2-2\ell q_2q_4)v_1v_2+q_2^2v_2^2]$$

$$-\frac{\gamma}{u^*}[\{(\ell q_4-q_1)v_1-q_2v_2\}(\ell q_5-q_3)(b_1v_1^2+b_2v_1v_2+b_3v_2^2)$$

$$-\frac{\ell q_4v_1}{u^*}\{(\ell q_4-q_1)v_1-q_2v_2\}^2] + \text{H.O.T.} \qquad (33)$$

$$F_2 = \frac{1}{\beta K(1+mu^*)}[msK\beta(q_1v_1+q_2v_2+q_3v_3)(q_6v_1+q_7v_2+q_8v_3)$$

$$-\alpha_0sm^2(K-x^*)(q_1v_1+q_2v_2+q_3v_3)^2-cK\beta^2(q_4v_1+q_5v_3)(q_6v_1+q_7v_2+q_8v_3)$$

$$-m\alpha_0\beta c(K-x^*)(q_1v_1+q_2v_2+q_3v_3)(q_4v_1+q_5v_3)-m\alpha_0\beta c(q_1v_1+q_2v_2)q_4^2v_1^2$$

$$-(1+mu^*)(q_4v_1+q_5v_3)^2]\left[1-\frac{m(q_1v_1+q_2v_2+q_3v_3)}{1+mu^*}\right] + \text{H.O.T.}$$

$$= \frac{1}{\beta K(1+mu^*)}[\{msK\beta q_1q_6-\alpha_0sm^2(K-x^*)q_1^2-cK\beta^2q_4q_6-m\alpha_0\beta c(K-x^*)q_1q_4$$

$$-(1+mu^*)q_4^2\}v_1^2+\{msK\beta(q_1q_7+q_2q_6)-\alpha_0sm^2(K-x^*)2q_1q_2-cK\beta^2q_4q_7$$

$$-m\alpha_0\beta c(K-x^*)q_2q_4\}v_1v_2+\{msK\beta q_2q_7-\alpha_0sm^2(K-x^*)q_2^2\}v_2^2]$$

$$+\frac{1}{\beta K(1+mu^*)}[msK\beta(b_1v_1^2+b_2v_1v_2+b_3v_2^2)\{(q_1q_8+q_3q_6)v_1+(q_2q_8+q_3q_7)v_2\}-$$

$$-\alpha_0 sm^2(K-x^*)2q_3(b_1v_1^2+b_2v_1v_2+b_3v_2^2)(q_1v_1+q_2v_2)-cK\beta^2\{q_4q_8v_1(b_1v_1^2$$

$$+b_2v_1v_2+b_3v_2^2)+q_5(q_6v_1+q_7v_2)(b_1v_1^2+b_2v_1v_2+b_3v_2^2)\}$$

$$-m\alpha_0\beta c(K-x^*)\{q_5(q_1v_1+q_2v_2)(b_1v_1^2+b_2v_1v_2+b_3v_2^2)+q_3q_4v_1(b_1v_1^2+$$

$$+b_2v_1v_2+b_3v_2^2)\}-m\alpha_0\beta c(q_1v_1+q_2v_2)q_4^2v_1^2-(1+mu^*)2q_4q_5v_1(b_1v_1^2+b_2v_1v_2+b_3v_2^2]$$

$$+\frac{1}{\beta K(1+mu^*)}\left\{-\frac{m(q_1v_1+q_2v_2)}{1+mu^*}\right\}[\{msK\beta q_1q_6-\alpha_0 sm^2(K-x^*)q_1^2-cK\beta^2q_4q_6$$

$$-m\alpha_0\beta c(K-x^*)q_1q_4-(1+mu^*)q_4^2\}v_1^2+\{msK\beta(q_1q_7+q_2q_6)-\alpha_0 sm^2(K-x^*)2q_1q_2$$

$$-cK\beta^2q_4q_7-m\alpha_0\beta c(K-x^*)q_2q_4\}v_1v_2+\{msK\beta q_2q_7-\alpha_0 sm^2(K-x^*)q_2^2\}v_2^2 \quad + \text{H.O.T.} \tag{34}$$

and

$$F_3 = \frac{1}{\beta K(1+mu^*)}[\alpha_0 sm^2(K-x^*)(q_1v_1+q_2v_2+q_3v_3)^2-m\alpha_0\beta c(K-x^*)(q_1v_1+q_2v_2$$

$$+q_3v_3)(q_4v_1+q_5v_3)+cK\beta^2(q_4v_1+q_5v_3)(q_6v_1+q_7v_2+q_8v_3)-ms\beta K(q_1v_1$$

$$+q_2v_2+q_3v_3)(q_6v_1+q_7v_2+q_8v_3)]\left\{1-\frac{m(q_1v_1+q_2v_2+q_3v_3)}{1+mu^*}\right\}$$

$$=\frac{1}{\beta K(1+mu^*)}[\theta_1v_1^2+\theta_2v_1v_2+\theta_3v_2^2]+\frac{1}{\beta K(1+mu^*)}[\alpha_0 sm^2(K-x^*)2q_3v_3(q_1v_1+$$

$$+q_2v_2)-m\alpha_0\beta c(K-x^*)\{(q_1v_1+q_2v_2)q_5v_3+q_3q_4v_1v_3\}+cK\beta^2\{q_4q_8v_1v_3$$

$$+q_5v_3(q_6v_1+q_7v_2)\}-ms\beta K\{(q_1v_1+q_2v_2)q_8+(q_6v_1+q_7v_2)q_3\}v_3]$$

$$+\frac{1}{\beta K(1+mu^*)}\left\{-\frac{m(q_1v_1+q_2v_2)}{1+mu^*}\right\}[\theta_1v_1^2+\theta_2v_1v_2+\theta_3v_2^2] + \text{H.O.T.} \tag{35}$$

where

$$\theta_1 = \alpha_0 sm^2(K-x^*)q_1^2 - m\alpha_0\beta c(K-x^*)q_1q_4 + cK\beta^2 q_4q_6 - ms\beta Kq_1q_6$$

$$\theta_2 = \alpha_0 sm^2(K-x^*)2q_1q_2 - m\alpha_0\beta c(K-x^*)q_2q_4 + cK\beta^2 q_4q_7 - msK\beta(q_1q_7+q_2q_6) \qquad (36)$$

$$\theta_3 = \alpha_0 sm^2(K-x^*)q_2^2 - ms\beta Kq_2q_7$$

We can now compute various partial derivatives. From (31)

$$G_{11}^{(1)} = L_1(2b_1) + \frac{1}{Q}\Bigg[\frac{-2\gamma w_1}{u^*}\left\{\ell^2q_4^2+q_1^2-2\ell q_1q_4\right\} + \frac{2w_2}{\beta K(1+mu^*)}\{msK\beta q_1q_6$$
$$-\alpha_0 sm^2(K-x^*)q_1^2-cK\beta^2q_4q_6-m\alpha_0\beta c(K-x^*)q_1q_4-(1+mu^*)q_4^2\}$$
$$+\frac{2w_3}{\beta K(1+mu^*)}\{2\theta_1\}\Bigg] \equiv d_1 \quad \text{(say)} \qquad (37)$$

$$G_{12}^{(1)} = L_1(b_2) + \frac{1}{Q}\Bigg[-\frac{\gamma w_1}{u^*}(2q_1q_2-2\ell q_2q_4) + \frac{w_2}{\beta K(1+mu^*)}\{msK\beta(q_1q_7$$
$$+q_2q_6)-\alpha_0 sm^2(K-x^*)2q_1q_2-cK\beta^2q_4q_7-m\alpha_0\beta c(K-x^*)q_2q_4\}$$
$$+\frac{w_3}{(1+mu^*)\beta K}\{\theta_2\}\Bigg] \equiv d_2 \quad \text{(say)} \qquad (38)$$

$$G_{22}^{(1)} = L_1(2b_3) + \frac{1}{Q}\Bigg[-\frac{2\gamma w_1}{u^*}q_2^2 + \frac{2w_2}{\beta K(1+mu^*)}\{msK\beta q_2q_7-\alpha_0 sm^2(K-x^*)q_2^2\}$$
$$+\frac{2w_3}{\beta K(1+mu^*)}\{\theta_3\}\Bigg] \equiv d_3 \quad \text{(say)} \qquad (39)$$

$$G_{111}^{(1)} = -\frac{w_1\gamma}{Qu^*}\left[(\ell q_5-q_3)6b_1(\ell q_4-q_1)-\frac{6\ell q_4}{u^*}(\ell q_4-q_1)^2\right]$$
$$+\frac{w_2}{Q\beta K(1+mu^*)}[6msK\beta(q_1q_8+q_3q_6)b_1-6\alpha_0 sm^2(K-x^*)2q_3b_1q_1$$
$$-6cK\beta^2\{q_4q_8b_1+q_5q_6b_1\}-m\alpha_0\beta c(K-x^*)\{6q_5q_1b_1+6q_3q_4b_1\}$$
$$-6m\alpha_0\beta cq_1q_4^4-12(1+mu^*)q_4q_5b_1] -$$

$$- \frac{w_2 m}{Q\beta K(1+mu^*)^2} \cdot 6q_1\{msK\beta q_1 q_6 - \alpha_0 sm^2(K-x^*)q_1^2 - cK\beta^2 q_4 \cdot q_6$$

$$- m\alpha_0 \beta c(K-x^*)q_1 q_4 - (1+mu^*)q_4^2\}$$

$$+ \frac{w_3}{Q\beta K(1+mu^*)} [12\alpha_0 sm^2(K-x^*) \cdot q_3 b_1 q_1 - 6m\alpha_0 \beta c(K-x^*)\{q_1 q_5 b_1 + q_3 q_4 b_1\}$$

$$+6cK\beta^2\{q_4 q_8 b_1 + q_5 q_6 b_1\} - 6ms\beta K b_1(q_1 q_8 + q_3 q_6)] - \frac{w_3 m_6}{Q\beta K(1+mu^*)^2} q_1 \theta_1 \equiv d_4 \tag{40}$$

$$G^{(1)}_{222} = - \frac{w_1 \gamma}{Qu^*} [-6(\ell q_5 - q_3)b_3 q_2] + \frac{w_2}{Q\beta K(1+mu^*)} [6msK\beta b_3(q_2 q_8 + q_3 q_7)$$

$$-6\alpha_0 sm^2(K-x^*)2q_3 b_3 q_2 - 6cK\beta^2\{q_5 q_7 b_3\} - 6m\alpha_0 \beta c(K-x^*)\{q_5 q_2 b_3\}]$$

$$- \frac{w_2 m}{Q\beta K(1+mu^*)^2} 6q_2\{msK\beta q_2 q_7 - \alpha_0 sm^2(K-x^*)q_2^2\}$$

$$+ \frac{w_3}{Q\beta K(1+mu^*)} [6\alpha_0 sm^2(K-x^*)2q_3 b_3 q_2 - m\alpha_0 \beta c(K-x^*)6q_2 q_5 b_3 + 6cK\beta^2 q_5 b_3 q_7$$

$$-6ms\beta K b_3\{q_2 q_8 + q_3 q_7\}] - \frac{mw_3}{Q\beta K(1+mu^*)^2}\{6q_2 \theta_3\} \equiv d_5 \quad \text{(say)} \tag{41}$$

$$G^{(1)}_{112} = - \frac{\gamma w_1}{Qu^*} [2(\ell q_5 - q_3)\{-b_1 q_2 + b_2(\ell q_4 - q_1) + \frac{4\ell q_4}{u^*}\{q_2(\ell q_4 - q_1)\}]$$

$$+ \frac{w_2}{Q\beta K(1+mu^*)} [2msK\beta\{b_1(q_2 q_8 + q_3 q_7) + b_2(q_1 q_8 + q_3 q_6)\}$$

$$-2\alpha_0 sm^2(K-x^*)2q_3\{b_1 q_2 + b_2 q_1\} - 2cK\beta^2\{q_4 q_8 b_2 + q_5 q_6 b_2 + q_5 q_7 b_1\}$$

$$-2m\alpha_0 \beta c(K-x^*)\{q_5 q_1 b_2 + q_5 q_2 b_1 + q_3 q_4 b_2\} - 2m\alpha_0 \beta c q_2 q_4^2 - 4(1+mu^*)q_4 q_5 b_2]$$

$$- \frac{2w_2 m}{Q\beta K(1+mu^*)^2} [q_1\{msK\beta(q_1 q_7 + q_2 q_6) - \alpha_0 sm^2(K-x^*)2q_1 q_2 - cK\beta^2 q_4 q_7$$

$$-m\alpha_0 \beta c(K-x^*)q_2 q_4\} + q_2\{msK\beta q_1 q_6 - \alpha_0 sm^2(K-x^*)q_1^2 - cK\beta^2 q_4 q_6$$

$$-m\alpha_0\beta c(K-x^*)q_1-(1+mu^*)q_4^2\}] + \frac{w_3}{Q\beta K_2(1+mu^*)}[2\alpha_0 sm^2(K-x^*)2q_3\{q_1b_2$$

$$+q_2b_1\}-2m\alpha_0\beta c(K-x^*)\{(q_1b_1+q_2b_1)q_5+q_3q_4b_2\}$$

$$+2cK\beta^2\{q_4q_8b_2+q_5(q_6b_2+q_7b_1)\}-2ms\beta K\{(q_1q_8+q_3q_6)b_2$$

$$+(q_2q_8+q_3q_7)b_1\}] - \frac{2w_3m}{Q\beta K(1+mu^*)^2}\{q_1\theta_2+q_2\theta_1\} \equiv d_6 \quad \text{(say)} \tag{42}$$

$$G^{(1)}_{122} = -\frac{\gamma w_1}{Qu^*}\left[2(\ell q_5-q_3)\{b_3(\ell q_4-q_1)-q_2b_2\} - \frac{2\ell q_4q_2^2}{u^*}\right]$$

$$+\frac{w_2}{Q\beta K(1+mu^*)}[2msK\beta\{b_2(q_2q_8+q_3q_7)+b_3(q_1q_8+q_3q_6)\}$$

$$-2\alpha_0 sm^2(K-x^*)2q_3\{b_2q_2+b_3q_1\}-2cK\beta^2\{q_4q_8b_3+q_5(q_6b_3+q_7b_2)\}$$

$$-2m\alpha_0\beta c(K-x^*)\{q_5(q_1b_3+q_2b_2)+q_3q_4b_3\}-2(1+mu^*)2q_4q_5b_3]$$

$$-\frac{2mw_2}{Q\beta K(1+mu^*)^2}[q_1\{msK\beta q_2q_7-\alpha_0 sm^2(K-x^*)q_2^2\}+q_2\{msK\beta(q_1q_7+q_2q_6)$$

$$-\alpha_0 sm^2(K-x^*)2q_1q_2-cK\beta^2q_4q_7-m\alpha_0\beta c(K-x^*)q_2q_4\}]$$

$$+\frac{w_3}{Q\beta K(1+mu^*)}[2\alpha_0 sm^2(K-x^*)2q_3\{b_3q_1+q_2b_2\}-2m\alpha_0\beta c(K-x^*)\{(q_1b_3$$

$$+q_2b_2)q_5+q_3q_4b_3\}+2cK\beta^2\{q_4q_8b_3+q_5(q_6b_3+q_7b_2)\}-2ms\beta K\{b_3(q_1q_8$$

$$+q_3q_6)+b_2(q_2q_8+q_3q_7)\}] - \frac{2mw_3}{Q\beta K(1+mu^*)^2}\{q_1\theta_3+q_2\theta_2\} \equiv d_7 \quad \text{(say)} \tag{43}$$

Observing the symmetry in (31) and (32) we find that the corresponding partial derivatives of $G^{(2)}$ can be obtained by making the following changes

$$L_1 \to L_2, \quad w_1 \to w_4, \quad w_2 \to w_5 \quad \text{and} \quad w_3 \to w_6$$

in (37), (38), (39), (40), (41), (42) and (43). Let us denote

$$G_{11}^{(2)} = e_1, \quad G_{12}^{(2)} = e_2, \quad G_{22}^{(2)} = e_3, \quad G_{111}^{(2)} = e_4$$

$$G_{222}^{(2)} = e_5, \quad G_{112}^{(2)} = e_6 \quad \text{and} \quad G_{122}^{(2)} = e_7.$$

Then using the formula (28), we conclude that if

$$\frac{3\pi}{4\sqrt{a_2}} \{d_4+d_7+e_6+e_5\} + \frac{3\pi}{4a_2} \{-d_1d_2 + e_3e_2 + e_1e_2 - d_3d_2+d_1e_1-d_3e_3\} < 0$$

Then the periodic orbits occur for $\alpha > \alpha_0$ and are asymptotically stable. But if the above expression is positive then the periodic orbits occur for $\alpha < \alpha_0$ and are unstable.